

SYSTEMATICS AND REPRODUCTIVE BIOLOGY OF THE CENTRAL AMERICAN SPECIES OF THE *APHELANDRA PULCHERRIMA* COMPLEX (ACANTHACEAE)¹

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ABSTRACT

Aphelandra (Acanthaceae) is a neotropical genus of about 170 species of herbs, shrubs, and small trees. The *A. pulcherrima* complex is a monophyletic group of about 40 species distinguished by the presence of bracteal nectaries and a unique corolla morphology. Thirteen Central American species belonging to this complex are recognized based on herbarium, field, and greenhouse studies; pollen morphology; and artificial hybridizations. The genus *Aphelandra* and the *A. pulcherrima* complex probably originated in South America. Central American species have evolved from South American or intermediate Central American ancestors. The species treated here are diffusely branched shrubs or sparsely branched, monocaulous plants. They are found in primary forest to disturbed secondary and edge habitats, and from low to middle elevations. Field observations indicate that all species produce odorless flowers that last a single day, produce copious, rather dilute nectar, and are hummingbird pollinated. All but *A. deppeana* are pollinated by large hermit hummingbirds (Trochilidae: Phaethorninae) or hermit-like species. The long, decurved bills and traplining foraging habits of these birds correspond to the floral morphology and spatial distribution of the plants. Chromosome data are not systematically useful within the group studied. All 12 species for which counts were obtained have $n = 14$ chromosomes. The 13 species are variable palynologically, showing three distinct pollen types, as well as significant variability in pollen size (length and width). Pollen characters resolve all but two species and provide evidence for patterns of phylogenetic relationships among the species. Although hybrids between many species pairs can be readily synthesized, hybrids in nature are rare. Four isolating mechanisms in addition to allopatry and intersterility are identified as potentially important among Central American *Aphelandras*. The paucity of naturally occurring hybrids is in most cases due to more than one type of barrier. Putative hybrids between *A. sinclairiana* and *A. gracilis*, and between *A. sinclairiana* and *A. golfodulcensis* have been found in the field. Artificial disturbance has apparently been important in creating situations favorable for hybridization between at least one of these pairs of species. Phylogenetic analysis identifies two main lineages within the group: Group I (*A. terryae*, *A. sinclairiana*, *A. storkii*, *A. gracilis*, *A. golfodulcensis*, *A. panamensis*, and *A. deppeana*) and Group II (*A. lingua-bovis*, *A. leonardii*, *A. laxa*, *A. campanensis*, *A. hartwegiana*, and *A. darienensis*). These results are in accord with data from artificial hybridizations, except that phylogenetic analysis indicates that the species of Group II are as closely interrelated as those of Group I, whereas crossability indices suggest that these species are much more distantly related. Genetic incompatibility may be an important barrier to interbreeding between species of Group II such that the results of artificial hybridizations do not provide reliable estimates of the degree of relationship among these species.

Aphelandra (Acanthaceae) is a morphologically diverse genus traditionally distinguished by its lack of cystoliths and possession of four monothealous anthers, bilabiate corollas, and elongate, tricolpate pollen grains. The more than

160 species are confined to the New World tropics, ranging from northern Argentina and Bolivia to northern Mexico. Over two-thirds of the taxa are confined to South America with notable concentrations of species in southeastern Brazil, Co-

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lombia, and Peru (Wasshausen, 1975). Thirty to 40 species are found in Central America and Mexico.

Aphelandra has been treated in several regional floras (Leonard, 1938, 1953, 1954; Gibson, 1974; Durkee, 1978), and in a recent monograph (Wasshausen, 1975). Knowledge of many of the species and of phylogenetic relationships among species, however, remains fragmentary. Many taxa are known only from one or very few, frequently incomplete specimens, and data from field and experimental studies are essentially lacking.

This study is a systematic investigation of the Central American species of the *Aphelandra pulcherrima* complex. The complex is an apparently monophyletic assemblage of about 40 species. As treated here, 13 of these species occur in Central America. New data from several sources have been gathered: comparative morphology of living plants, field observations, chromosome counts, palynology, studies of floral biology, and artificial hybridizations. The taxonomic treatment is based on these data and portrays the best hypothesis for the phylogenetic relationships among these species.

SYSTEMATIC POSITION AND TAXONOMIC HISTORY

The Acanthaceae are a large, predominantly tropical family with about 250 genera and 2,600 species (Long, 1970; Heywood, 1978). The family is pantropical with four centers of distribution: Indomalaysia, Africa, Brazil, and Central America (Long, 1970). Whereas most acanth genera are restricted to one continent, a few are pantropical (e.g., *Justicia*, *Ruellia*).

Taxonomists have almost unanimously considered Acanthaceae to be closely related to Scrophulariaceae. These two families, along with Bignoniaceae, Lentibulariaceae, Gesneriaceae, Pedaliaceae, several other small families, and a varying group of families of disputed affinities, have usually been classified together at the ordinal level (e.g., Scrophulariales: Stebbins, 1974; Takhtajan, 1969; Cronquist, 1968, 1981; Bignoniales: Thorne, 1976; Tubiflorae: Engler, 1964; Personales: Hutchinson, 1973). Although the phylogenetic relationships of all of these families have not yet been fully studied, it is likely that several families are not strictly monophyletic (sensu Hennig, 1966: strictly monophyletic taxa must include all and only the descendants of a

common ancestral species). For example, because Orobanchaceae are probably derived from within Scrophulariaceae, the latter family is not strictly monophyletic. Confident recognition of strictly monophyletic families and placement of disputed groups must await phylogenetic analysis at the ordinal level.

Acanthaceae provide an excellent example of the unresolved relationships encountered in the order. Considerable disagreement exists as to the taxonomic placement of the groups recognized by Lindau (1895) as subfamilies of Acanthaceae: Nelsonioideae, Thunbergioideae, Mendoncioideae, and Acanthoideae. Bremekamp (1953, 1965) systematically reviewed the evidence for taxonomic placement of these groups and concluded that Nelsonioideae should be transferred to Scrophulariaceae (near Rhinanthaeae) and that the remaining three subfamilies should be recognized at the familial level. Mohan Ram and Wadhi (1964, 1965) favored retention of Nelsonioideae in Acanthaceae on the basis of embryological characters, and emphasized similarities between this group and Andrographideae. Thunbergioideae are embryologically distinct from Acanthaceae, justifying, in their view, Bremekamp's recognition of the group as a family. Embryological data are lacking for Mendoncioideae. After morphological and anatomical study of the genera comprising Nelsonioideae (sensu Lindau), Hossain (1971) returned this group to Acanthaceae as a tribe (Nelsonieae) near Andrographideae. Hossain also took exception to Bremekamp's removal and elevation to familial status of Mendoncioideae and Thunbergioideae, but presented no new evidence. Cuticular studies demonstrate that all four of Lindau's subfamilies share diacytic stomates (Ahmad, 1974a, 1974b). This evidence suggests recognition of a monophyletic taxon composed of the four groups, but diacytic stomates occur sporadically throughout the Scrophulariales (Metcalf & Chalk, 1950). Shared possession of odd panduriform trichomes suggests a relationship between Thunbergioideae and Nelsonioideae (Ahmad, 1978). Based on a study of epidermal hairs of 109 species in 39 genera from all subfamilies, Ahmad (1978) favored retention of Lindau's subfamilies within Acanthaceae. There is thus considerable disagreement as to the exact familial limits of Acanthaceae, as well as lack of consensus regarding relationships among the four clearly circumscribed groups.

There is little doubt, however, that Acantha-

TABLE 1. Characters distinguishing Bremekamp's subfamilies of Acanthaceae.

Character	Acanthoideae	Ruellioideae
Shoots	Never articulated	Always articulated
Cystoliths	Absent	Present ^a
Stamens	4	2 or 4
Anthers	Monothealous ^a	At least 2 bithealous
Pollen	Colpate	Colporate or porate ^a
Tribes included	Hasselhoffiae Rhombochlamydeae Stenandriopsidae Aphelandreae Acantheae	Trichanthereae Whitfieldiae Louteridae Ruelliae Lepidagathideae Andrographideae Justiceae

^a Hypothesized derived character states.

ceae (sensu Bremekamp, Lindau's Acanthoideae) are a closely related group sharing several derived characters: ovary bilocular with two longitudinal rows of ovules in each locule, capsule loculicidal and explosively dehiscent with the exalbuminous seeds supported by well-developed retinacula. Whether Acanthaceae thus delimited are strictly monophyletic will be determined only by analysis of sister group relationships at the family level within the order.

Several systems of classification for subdivision of Acanthaceae (sensu Bremekamp) have been proposed, with emphasis on pollen characters. Nees von Esenbeck (1847a) recognized 11 tribes within his "suborder" Echmatacantheae, which included the genera currently placed in Acanthaceae sensu stricto. Bentham and Hooker (1876) divided these genera among three tribes: Ruelliae, Acantheae, and Justiceae. Lindau's (1895) Acanthoideae was divided into two "series" (= supertribes): Contortae (corolla aestivation usually convolute) with seven tribes, and Imbricatae (corolla aestivation usually imbricate) with ten tribes. More recently, Bremekamp (1965) recognized two subfamilies, Acanthoideae and Ruellioideae, that are distinguished by differences in several characters (Table 1), and comprise five and seven tribes, respectively. Although intrafamilial classification of Acanthaceae has not been a major aspect of this study, I provisionally accept Bremekamp's system as best representing the probable phylogenetic relationships among genera in this family. Both subfamilies are distinguished by apparently derived character states (e.g., monothealous anthers

in Acanthoideae, cystoliths and colporate or porate pollen in Ruellioideae).

Of the tribes comprising Bremekamp's Acanthoideae, the Acantheae and Aphelandreae are well-defined groups of genera that share one or more derived character states (Bremekamp, 1965) and are probably monophyletic. The remaining tribes, however, bear further investigation. All three resemble either Acantheae or Aphelandreae and are separated from these only by one or a few character states that appear to be primitive within the subfamily. Stenandriopsidae, for example, are separated from Aphelandreae by possession of a subactinomorphic corolla (versus a strongly zygomorphic corolla in the latter tribe), and from Acantheae by lack of the characteristic incision at the adaxial side of the corolla. Further study of these small, geographically restricted groups might provide evidence that they are relatively primitive members of either Acantheae or Aphelandreae. These latter two tribes are probably sister groups (sensu Hennig, 1966), but the phylogenetic relationships within the subfamily bear further study.

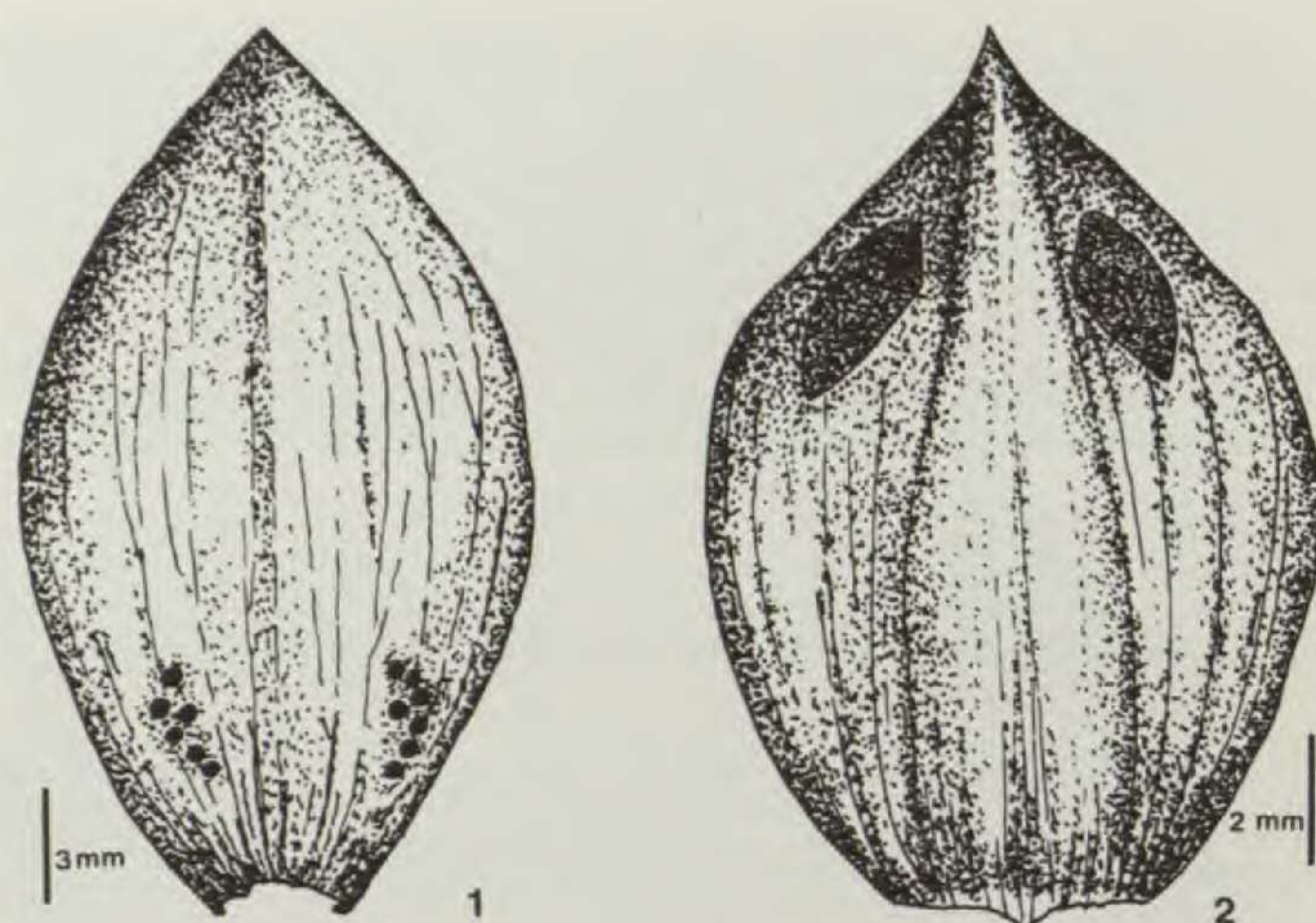
There is little disagreement as to taxonomic placement of *Aphelandra*. It is related to the Old World genus *Acanthus* and these, together with a group of allied genera, have been placed in the single tribe Acantheae (Bentham & Hooker, 1876) or segregated into two related tribes. Nees von Esenbeck (1847a) recognized two adjacent tribes, Aphelandreae and Acantheae, in his "series" (= supertribe) Imbricatae. Bremekamp (1965) follows this alignment, placing both tribes in his subfamily Acanthoideae as discussed above (Ta-

ble 1). Neotropical genera allied with *Aphelandra* in Aphelandreae include *Cyphacanthus*, *Neria-canthus*, *Encephalosphaera*, *Stenandrium*, and *Holographis*. The phylogenetic relationships among these genera, however, have yet to be rigorously investigated and one or more might be more correctly placed within *Aphelandra*. *Encephalosphaera*, for example, has been distinguished from *Aphelandra* only on the basis of pollen characters. A broader palynological survey of *Aphelandra* (Wasshausen, 1975; McDade, unpubl. data) indicates that pollen variability is much greater than was known to Lindau when he described *Encephalosphaera*.

Plants currently placed in *Aphelandra* were first described in *Justicia* by Jacquin in 1762 and Vahl in 1794 (Wasshausen, 1975). *Aphelandra* was first proposed as a distinct genus by Robert Brown (1810) to include *J. pulcherrima* Jacq., *J. scabra* Vahl, and *J. cristata* Jacq. These species were distinguished from *Justicia* by their four unilocular anthers and calyx of five unequal segments. Rafinesque (1838) appears to have recognized the same differences when he erected the genus *Amathea* based on *J. pulcherrima* Jacq. In the first half of the nineteenth century, five additional genera were described that have since been considered congeneric with *Aphelandra*: *Synandra* Schrader (1821), *Strobilorrhachis* Klotzsch (1839), *Hydromestus* Scheidweiler (1842a), *Hemisandra* Scheidweiler (1842b), and *Lagochilium* Nees von Esenbeck (1847a). A more detailed discussion of these segregate genera and relevant taxonomic decisions is found in Wasshausen (1975).

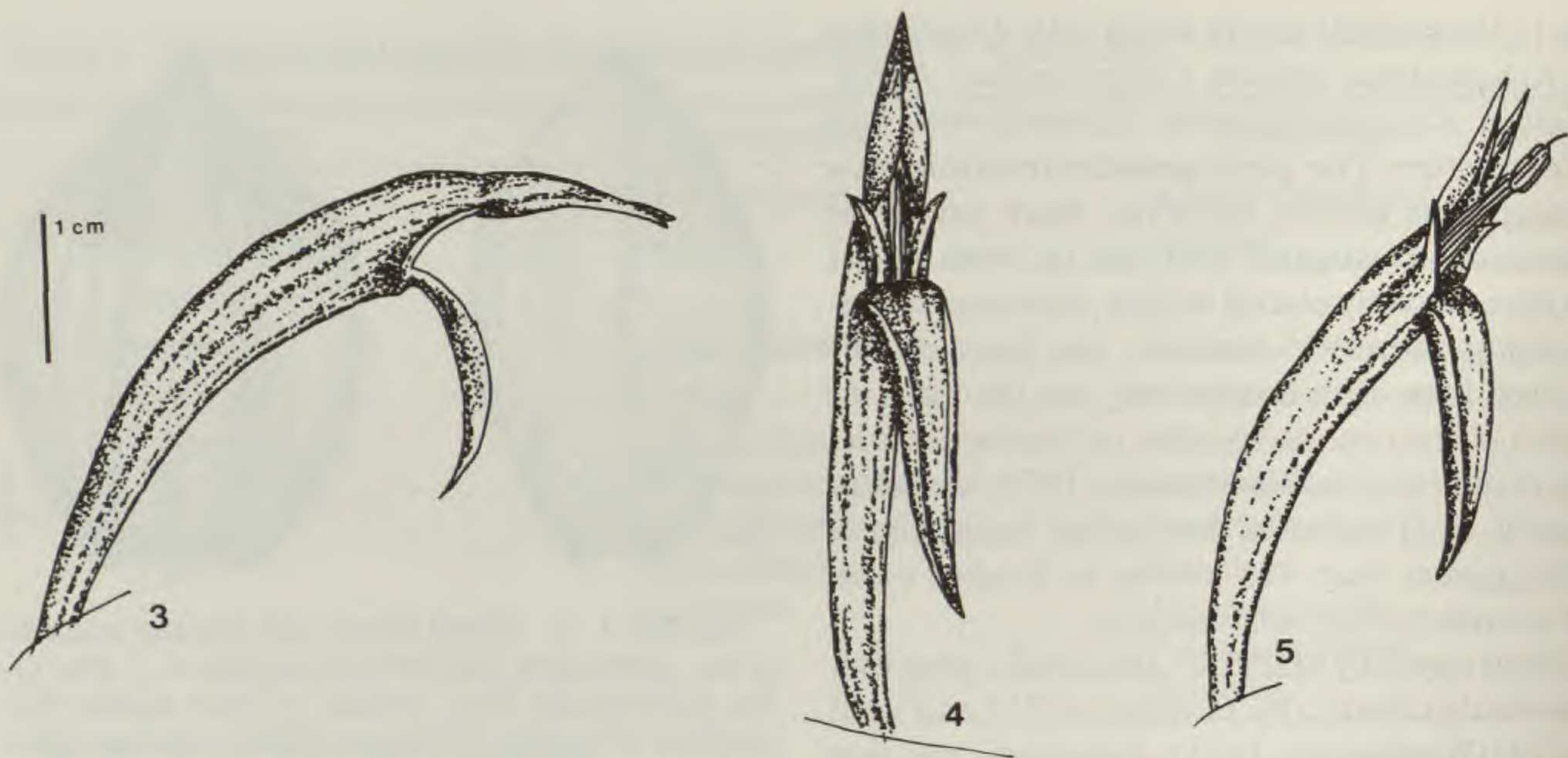
Many species have been described in *Aphelandra*, with notable contributions by Nees von Esenbeck (1847a, 1847b), Lindau (1893, 1895, 1904), Leonard (1938, 1953, 1961), and Wasshausen (1973a, 1973b, 1975). A recent revision of the entire genus (Wasshausen, 1975) recognized 165 species and two varieties. Two additional species were described by Durkee (1978). Three new species were recognized in the course of this study (McDade, 1982) and a previously recognized species is reduced to synonymy herein. Several regional treatments of the genus are available, including those for Costa Rica (Leonard, 1938), Colombia (Leonard, 1953), Guatemala (Gibson, 1974), and Panama (Durkee, 1978).

In the only published supraspecific classification of this large and variable genus, Nees von Esenbeck (1847a) recognized two sections based



FIGURES 1, 2. Floral bracts and bracteal nectaries in the *Aphelandra pulcherrima* complex.—1. Few (1–10), individually large, circular to oval glands characteristic of species of Group I: (1) *A. terryae*, (2) *A. sinclairiana*, (3) *A. storkii* (figured), (4) *A. gracilis*, (5) *A. golfodulcensis*, (6) *A. panamensis*, and (7) *A. deppeana*.—2. Oblong patches composed of many (>100) minute glands characteristic of species of Group II: (8) *A. lingua-bovis*, (9) *A. leonardii*, (10) *A. laxa*, (11) *A. campanensis*, (12) *A. hartwegiana* (figured), and (13) *A. darienensis*.

on relative length of the middle and lateral lobes of the lower corolla lip. In *Stenochila*, the lateral lobes were less than one-fourth as long as the middle lobe. Section *Platycheila* included species with lower corolla lobes more nearly equal. The latter section was divided further into two subsections, *Genuinae* and *Acanthoideae*, with entire and serrate or pinnately lobed leaves, respectively. Although Lindau (1895) followed Nees von Esenbeck's system in his treatment of the genus, subsequent systematists have not. It is apparent that there are several monophyletic groups within the genus, each of which can be recognized by several derived character states [e.g., the *A. pulcherrima* complex referred to by Leonard (1953) and treated in part here]. Several difficulties, however, have thus far frustrated attempts to devise a valid infrageneric classification of the genus. Many species are poorly known and are represented in herbaria by one or few specimens, which frequently lack mature inflorescences and flowers. In addition, several aspects of corolla morphology (including relative size and degree of fusion of the lobes, morphology of the upper lip at anthesis, and position of the anthers in relation to the corolla) are poorly preserved in most herbarium specimens and difficult to observe. Establishment of a natural supraspecific classification of the genus *Aphelandra*



FIGURES 3–5. Corolla morphology in the *Aphelandra pulcherrima* complex.—3. Lateral view, anthers and stigma concealed within folded lobes of upper lip.—4. Frontal view, note reduction of lateral lobes of lower lip, and anther pocket formed by folding of lobes of upper lip.—5. Anther pocket opened to reveal anthers and exerted stigma, note bilobed upper lip.

will be a valuable contribution to systematic knowledge of Acanthaceae.

DELIMITATION OF THE
APHELANDRA PULCHERRIMA SPECIES COMPLEX

This group of about 40 species forms a morphologically well-defined, monophyletic complex, with all members sharing several derived features including extrafloral nectaries on the bracts and a distinctive floral morphology. Nectaries are borne laterally and usually medially along both margins of the abaxial surface of the

floral bracts, and are of two distinct types: clumps of 1–10 relatively large (0.5–1.25 mm diam.) glands, or oblong patches (several mm diam.) of many (>100) extremely minute glands (Figs. 1, 2, respectively). Nectar production begins soon after the inflorescences are initiated and continues throughout the flowering period. Nectar is consumed by ants of many species and ants are rarely absent from inflorescences. Several unusual features of the corolla result in a very distinctive structure: the edges of the bilobed upper lip are laterally folded to form a pocket that par-

TABLE 2. Central American members of the *Aphelandra pulcherrima* species complex.

Species (Abbreviation)	Range
1. <i>A. terryae</i> Standley (TE)	E Panama and Colombia
2. <i>A. sinclairiana</i> Nees (SI)	Central Panama
3. <i>A. storkii</i> Leonard (ST)	Limón and Heredia, Costa Rica
4. <i>A. gracilis</i> Leonard (GR)	Central Panama
5. <i>A. golfodulcensis</i> McDade (GO)	SW Costa Rica and adjacent Panama
6. <i>A. panamensis</i> McDade (PA)	Central Panama
7. <i>A. deppeana</i> Schldl. & Cham. (DE)	S Mexico to N South America
<i>A. dukei</i> Wassh. (= <i>A. deppeana</i> Schldl. & Cham.)	
8. <i>A. lingua-bovis</i> Leonard (LB)	SW Costa Rica, Panama, and Colombia
9. <i>A. leonardii</i> McDade (LE)	Costa Rica and Panama
10. <i>A. laxa</i> Durkee (LA)	San Blas, Panama
11. <i>A. campanensis</i> Durkee (CA)	Central Panama
12. <i>A. hartwegiana</i> Nees ex Benth. (HA)	E Panama and Colombia
13. <i>A. darienensis</i> Wassh. (DA)	Darién, Panama

tially or completely conceals the anthers at anthesis, and the lateral lobes of the lower corolla lip are extremely reduced (to only 1–2 mm long) and flattened in a plane perpendicular to the tube so that they almost contact one another across the mouth of the tube (Figs. 3–5). This closed-mouth, concealed-anther morphology functions in pollination. A hummingbird inserts its bill into the corolla by using the tip of the bill to force apart the lateral corolla lobes. As the broadest, basal portion of the bill enters the corolla, the upper lip opens, bringing the anthers and exerted stigma into contact with the bird's head.

No other species of *Aphelandra* have both bracteal nectaries and the distinctive corolla morphology that characterize this complex. Shared possession of these derived morphological features provides strong evidence for a monophyletic origin of this group of species. Three South American species outside this complex possess bracteal nectaries: *A. lamprantha* Leonard, *A. impressa* Lindau, and *A. hylaea* Leonard. These species are probably the closest living relatives of the *A. pulcherrima* group, with one or more constituting the sister group of the *A. pulcherrima* complex.

The species belonging to this complex are identified in Appendix A. Nine species restricted to Central America and four found both in Central and northern South America are recognized as belonging to the *A. pulcherrima* complex (Table 2). The comparatively recent origin of the Central American isthmus compared to the older continent of South America, along with the clear Gondwana distribution pattern of Acanthaceae and the presence of close relatives of *Aphelandra* in Africa suggest a South American origin of the genus and of this species complex. The wholly Central American species are thus derived directly or through intermediate Central American ancestors from South American ancestors. Species found in both areas probably represent extensions of older South American ranges to include adjacent eastern Central America.

COMPARATIVE MORPHOLOGY

Habit and branching. The species of *Aphelandra* treated here have two distinct growth forms that are associated with distinctive arrangements of the inflorescences. Individuals of six species are relatively low plants characterized by a very soft-wooded central axis that branches only after differentiation of the growing point into an inflorescence (Fig. 6). The one or two



FIGURE 6. Monocaulous habit characteristic of six Central American species of the *Aphelandra pulcherrima* complex: (3) *A. storkii*, (8) *A. lingua-bovis*, (10) *A. laxa*, (11) *A. campanensis*, (12) *A. hartwegiana*, and (13) *A. darienensis*. (*Aphelandra storkii*, Finca La Selva, Heredia, Costa Rica.)

lateral branches subsequently formed are equal and, again, branch only after flowering. This pattern has been described by Troll (1935) as dichasial sympodial branching. Because the stems are soft-wooded (sometimes rather succulent), the branches invariably break after at most three branching points. As a consequence, individuals of species with this monocaulous growth form are mostly 1–2.5 m tall and very rarely larger than 3 m. The remaining seven species form true shrubs with generally profuse lateral branching (Fig. 7). Individuals of four species are soft-wooded shrubs that attain heights of 4–5 m. *Aphelandra gracilis* and *A. panamensis* are small trees to 7 m tall and 12 cm DBH. Individuals of *A. deppeana* tend to sprawl, forming horizontal branches close to the ground, and reach heights of 3–4 m. Plants of all species retained their characteristic habits when grown in greenhouses and



FIGURE 7. Shrubby habit characteristic of seven Central American species of the *Aphelandra pulcherrima* complex: (1) *A. terryae*, (2) *A. sinclairiana*, (4) *A. gracilis*, (5) *A. golfodulcensis*, (6) *A. panamensis*, (7) *A. deppeana*, and (9) *A. leonardii*. (*Aphelandra panamensis*, Cerro Jefe, Panamá, Panama.)

were unusual only in their tendency to flower profusely while very small.

Leaves. All species treated here have opposite, isophyllous leaves, with the exception of infrequent alternate-leaved individuals (or branches of individuals) of *A. terryae* and *A. golfodulcensis*. The leaves of most species have a well-differentiated blade and petiole, but those of *A. panamensis* and occasionally *A. deppeana* are sessile. Petioles are slender and similar in vestiture to the veins of the abaxial leaf surface. Leaves are simple, with entire, undulate or crenulate margins, and range from linear (in occasional plants of *A. deppeana*) through elliptic (most species) to obovate. Texture of the blades ranges from membranous to coriaceous to very slightly succulent, and from glabrous through moderately scabrous to densely pubescent. Trichomes of the adaxial and abaxial leaf surfaces are generally identical in type and length, but differ in density. Venation is pinnate with the costa generally depressed below the adaxial surface and protruding on the abaxial surface. Leaf surfaces are generally plane, but are slightly bul-

late in *A. storkii* and occasional individuals of *A. sinclairiana*. Except for variability in size, leaf variation over the range of each species appears to be minimal. However, Costa Rican plants of *A. leonardii* have leaves that differ from those of Panamanian plants in shape (narrower), vestiture (trichomes more dense), and texture (membranous rather than slightly succulent).

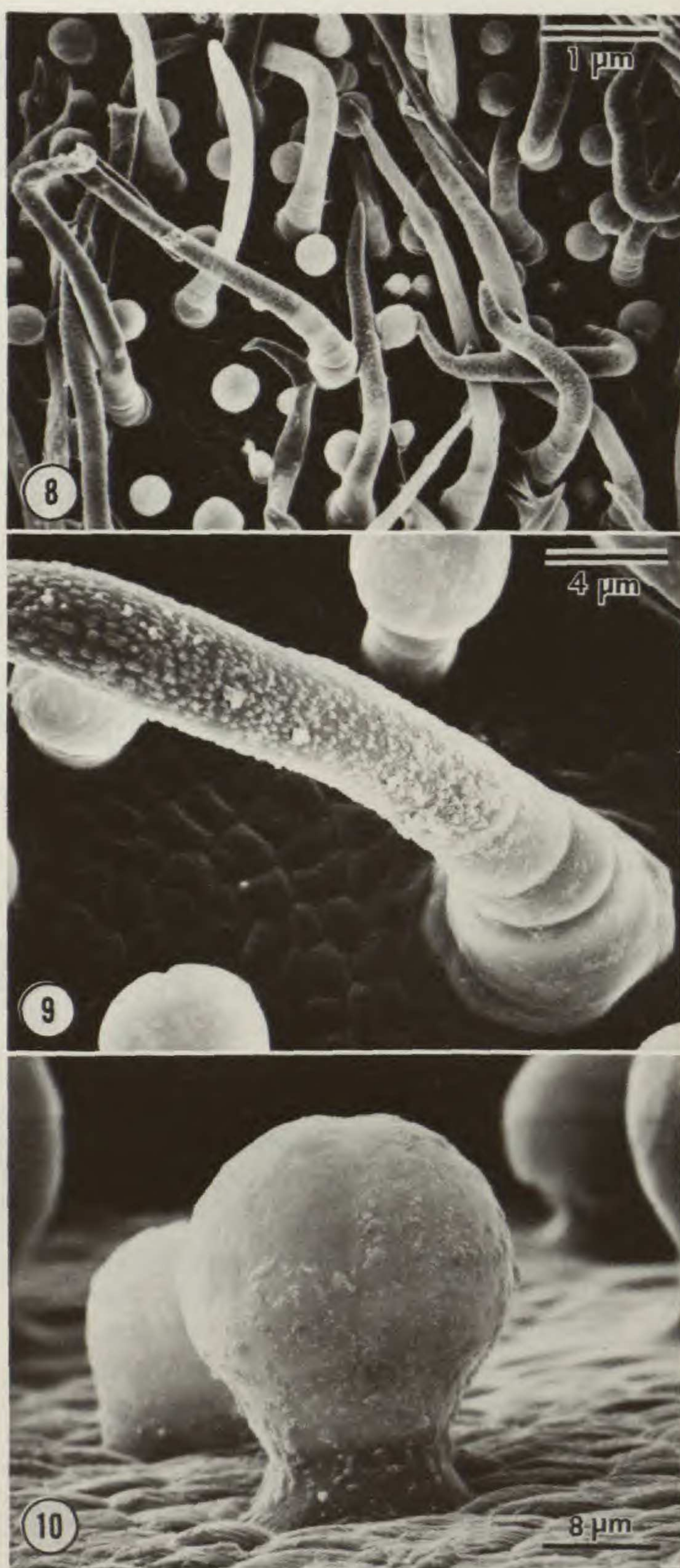
Vestiture. Two types of trichomes occur in the species treated here. Simple, uniseriate trichomes composed of 1–3 thin-walled basal cells, and a long (rarely septate), thick-walled terminal cell(s) are found in all species on at least some structures (Figs. 8, 9). The terminal cells are usually smooth, but may be short barbellate. In addition, multicellular, capitate to turbinate, presumably glandular trichomes are found in many species (Fig. 10). Trichomes of both types are widely distributed in Acanthaceae (Ahmad, 1978; Singh & Jain, 1975). Of taxonomic significance in the species treated here are the density, length and posture of simple trichomes on different plant structures, as well as the presence or absence of glandular trichomes.

Inflorescences. *Aphelandra* has spicate inflorescences with distichously arranged flowers, each subtended by a floral bract and two bracteoles. In the species treated here, two distinct arrangements of spikes are found that are correlated with plant habit. Species that branch freely to form true shrubs produce many spikes in a terminal, paniculate inflorescence. In species that branch rarely or not at all, inflorescences are simple or rarely composed of up to five spikes. Individual spikes of shrubby species are relatively short (10–20 cm) and few-flowered (12–40 per spike). Those of sparsely branched species are much longer (to 70 cm) and have many more flowers (to over 200 per spike). The arrangement of flowering spikes is of taxonomic significance and may have important implications for plant breeding systems as it relates to the number of flowers open daily per plant.

Floral bracts. The usually large and conspicuous bracts that subtend flowers of *Aphelandra* are highly variable among species and are traditionally important in identification systematics (Leonard, 1953; Wasshausen, 1975). All species treated here have extrafloral nectaries located laterally and usually medially along both margins of the floral bracts. As described above, two distinct types of nectaries occur (Figs. 1, 2). Additional taxonomically significant features of floral bracts are size, texture, color, apical shape, position of the nectaries and disposition along the rachis.

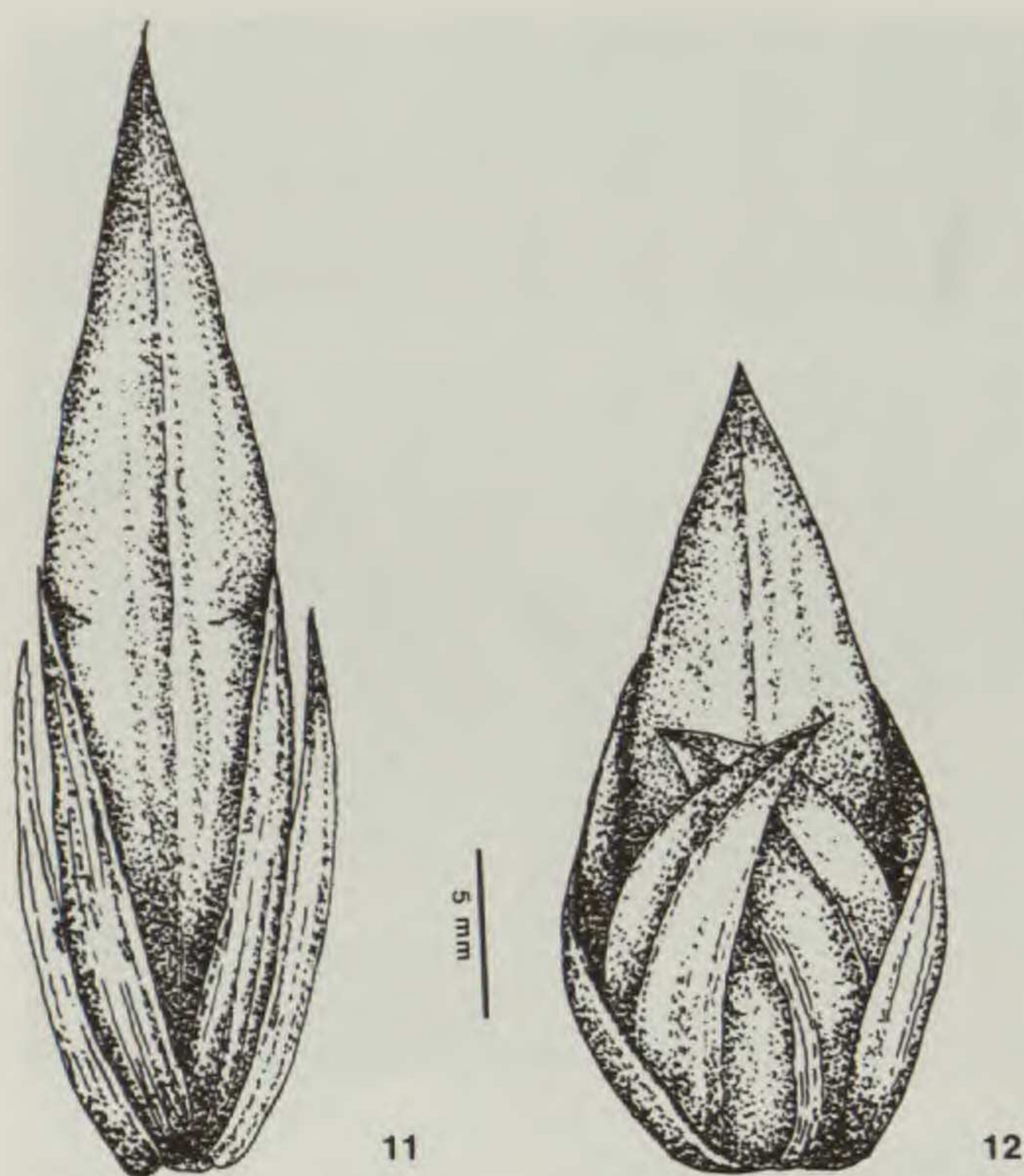
Species with nectaries composed of a few, large glands have bracts that are membranous and divergent from the rachis. *Aphelandra panamensis* and *A. deppeana* share imbricate bracts that are green and marginally toothed. *Aphelandra gracilis* and *A. golfodulcensis* have entire, green to dull orange, rather small and narrowly ovate bracts that are barely imbricate in the latter and quite lax in the former. The remaining species, *A. terryae*, *A. sinclairiana*, and *A. storkii*, have orange bracts that are closely imbricate. Bracts of *A. sinclairiana* and *A. terryae* are obtuse at the apex whereas those of the remaining species are acute. Bract size is an important character among these species, ranging from 5 mm long in *A. gracilis* to 25–30 mm long in *A. storkii*. *Aphelandra storkii* differs from the other species sharing large glands in having bracts that are coriaceous.

The floral bracts of species with minute glands are characteristically entire and leathery in tex-



FIGURES 8–10. Trichomes of Central American species of the *Aphelandra pulcherrima* complex (scanning electron photomicrographs, *A. hartwegiana*, McDade 425, DUKE).—8. Uniseriate and glandular trichomes of adaxial leaf surface.—9. Uniseriate trichomes showing basal cells and part of barbellate terminal cell, adaxial leaf surface.—10. Glandular turbinate trichome, abaxial leaf surface.

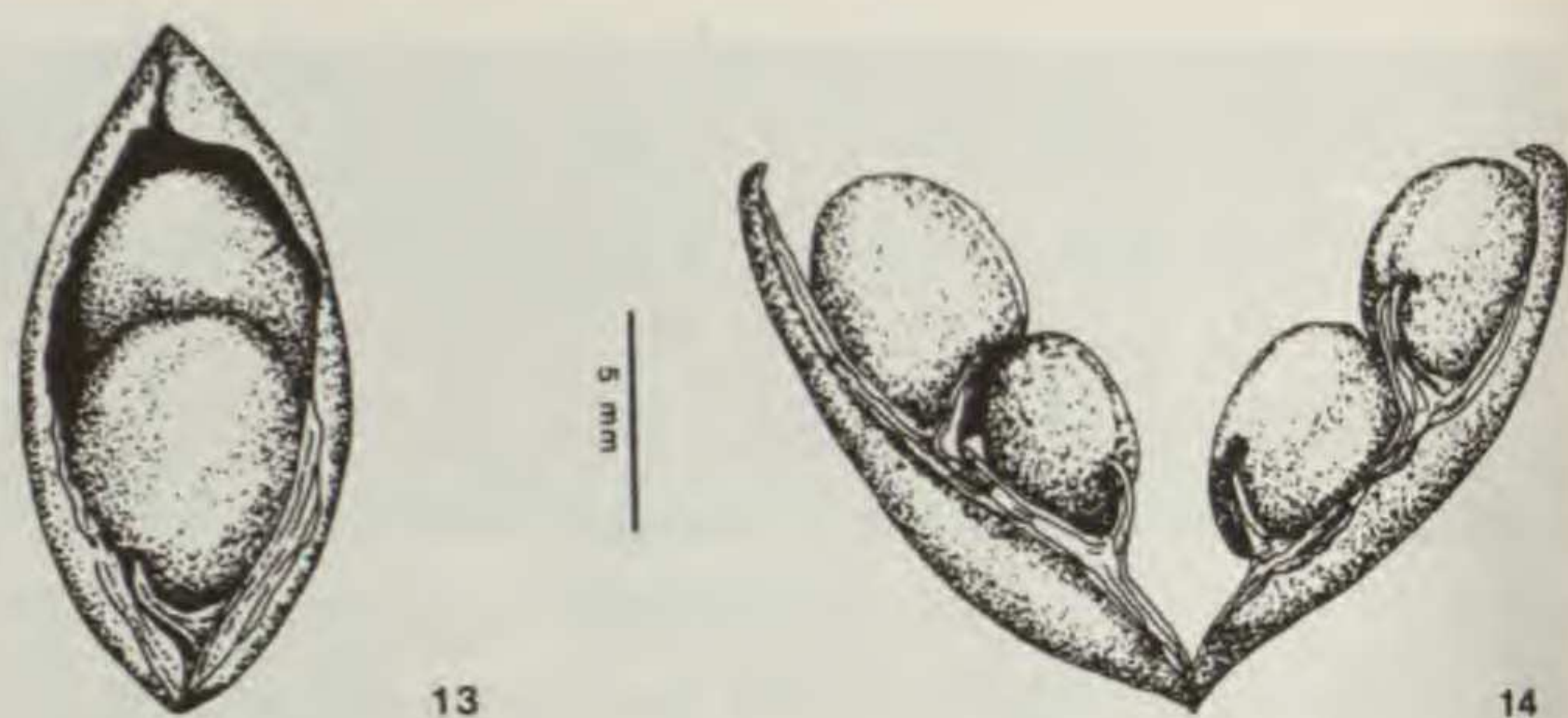
ture. Among these species, *A. lingua-bovis*, *A. leonardii*, and *A. campanensis* have rhombic-ovate bracts that are appressed to the rachis and nested among adjacent bracts, overlapping only



FIGURES 11, 12. Bracteoles of the *Aphelandra pulcherrima* complex.—11. Lanceolate, apically acute, sepal-like bracteoles most common in the group.—12. Falcate, keeled bracteoles found only in (11) *A. campanensis*, (12) *A. hartwegiana* (figured), and (13) *A. darienensis*.

slightly. *Aphelandra laxa* shares this pattern except that the bracts are laxly disposed. Flowers of these species wither and dry before falling from the plant because they are held tightly between the rachis and the close-fitting bracts. *Aphelandra hartwegiana* is similar but the bracts are broadly ovate and diverge from the rachis. Although it shares the glandular morphology of the above species, *A. darienensis* has bracts that are ovate, densely imbricate and apically arched away from the rachis.

Bracteoles. A pair of conspicuous lateral bracteoles subtend each flower in nearly all species of *Aphelandra* [in the remaining species, these structures are rudimentary (Leonard, 1953; Wasshausen, 1975)]. With three exceptions, bracteoles of the species treated here are lanceolate to narrowly ovate and are similar to the sepals in texture and apical shape (Fig. 11). In *A. hartwegiana*, the bracteoles are falcate and cross apically on the adaxial side of the corolla (Fig. 12). The bracteoles of *A. campanensis* and *A. darienensis* are similarly falcate, but do not overlap.

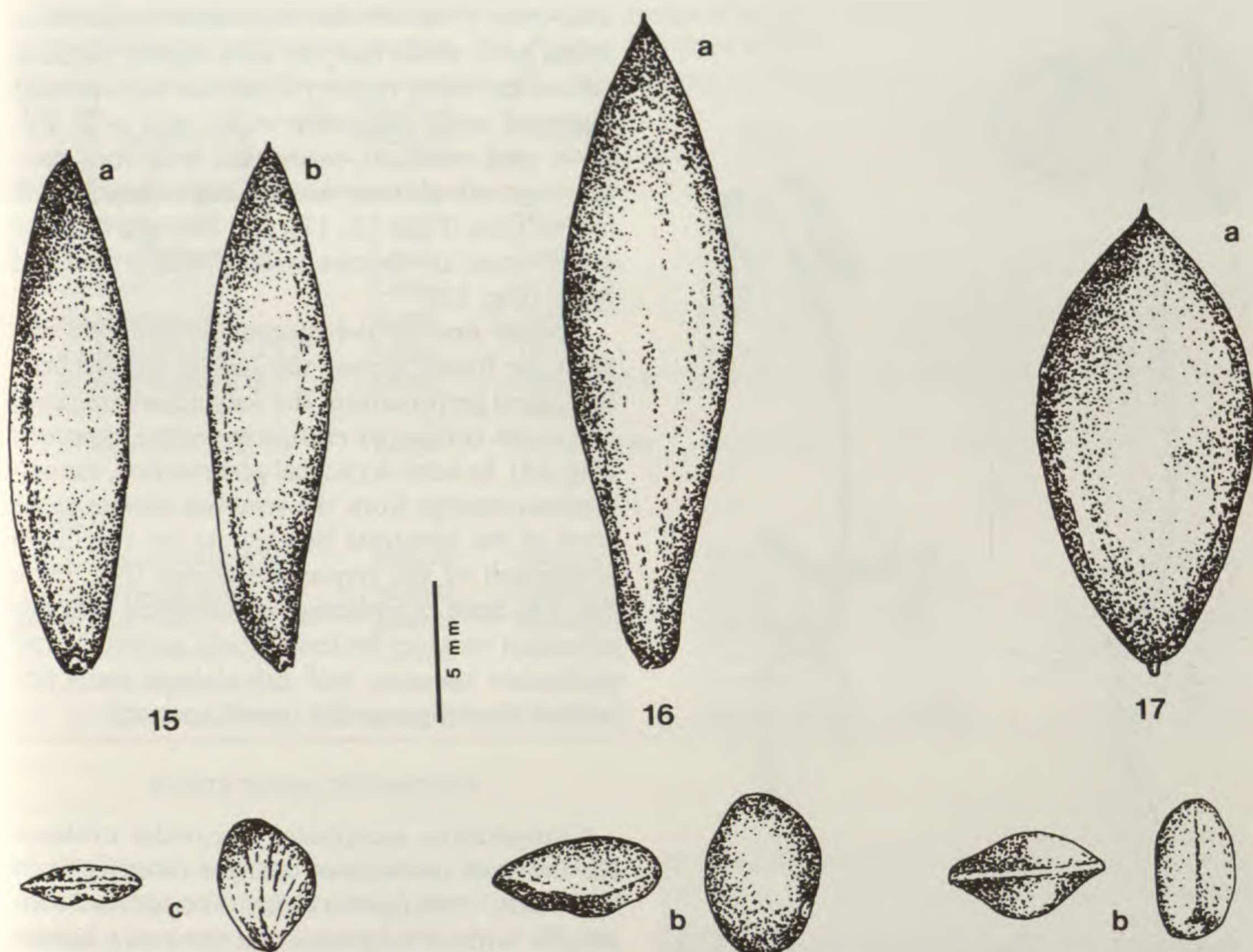


FIGURES 13, 14. Capsule morphology and dehiscence in *Aphelandra*.—13. Immature fruit opened to show one of two rows of two superposed seeds.—14. Dehiscent capsule with seeds held by woody retinacula (*A. deppeana* figured).

Calyx. Species of *Aphelandra* have a five-parted, polysepalous calyx with a wide adaxial segment, narrower paired abaxial segments and narrowest paired lateral segments. The species treated here are variable in calyx length, width, shape (oblong or lanceolate), shape at the apex (acute or obtuse and apiculate), and color (green to brightly colored).

Corolla. As described above, species of the *A. pulcherrima* complex share a unique and derived morphology of the upper and lower corolla lips (Figs. 3–5). The corolla tube in these species is constricted to 1–2 mm in diam. just above the ovary, which may protect the nectaries and ovary from sharp, probing bills of pollinating hummingbirds. This narrowed section is further congested and strengthened by the bases of the filaments, which are inserted in the tube just above the narrowest point. In five of the species treated here (*A. leonardii*, *A. laxa*, *A. campanensis*, *A. hartwegiana*, *A. darienensis*), corollas open by an abrupt downward movement of the lower lip. The lower lip remains plane and is strongly reflexed to lie parallel to the corolla tube. In the remaining eight species, the corolla lobes are more tightly imbricate in the bud and flowers open gradually or when visited by a pollinator. Additional corolla characters of taxonomic importance in this group of species include total length (36–75 mm), color, pubescence (glabrous to pilose), texture (membranous to quite coriaceous), and dimensions of the upper lip.

Androecium. All species of *Aphelandra* possess four monothecate, epipetalous stamens. The anthers are basifixed, erect and held parallel to



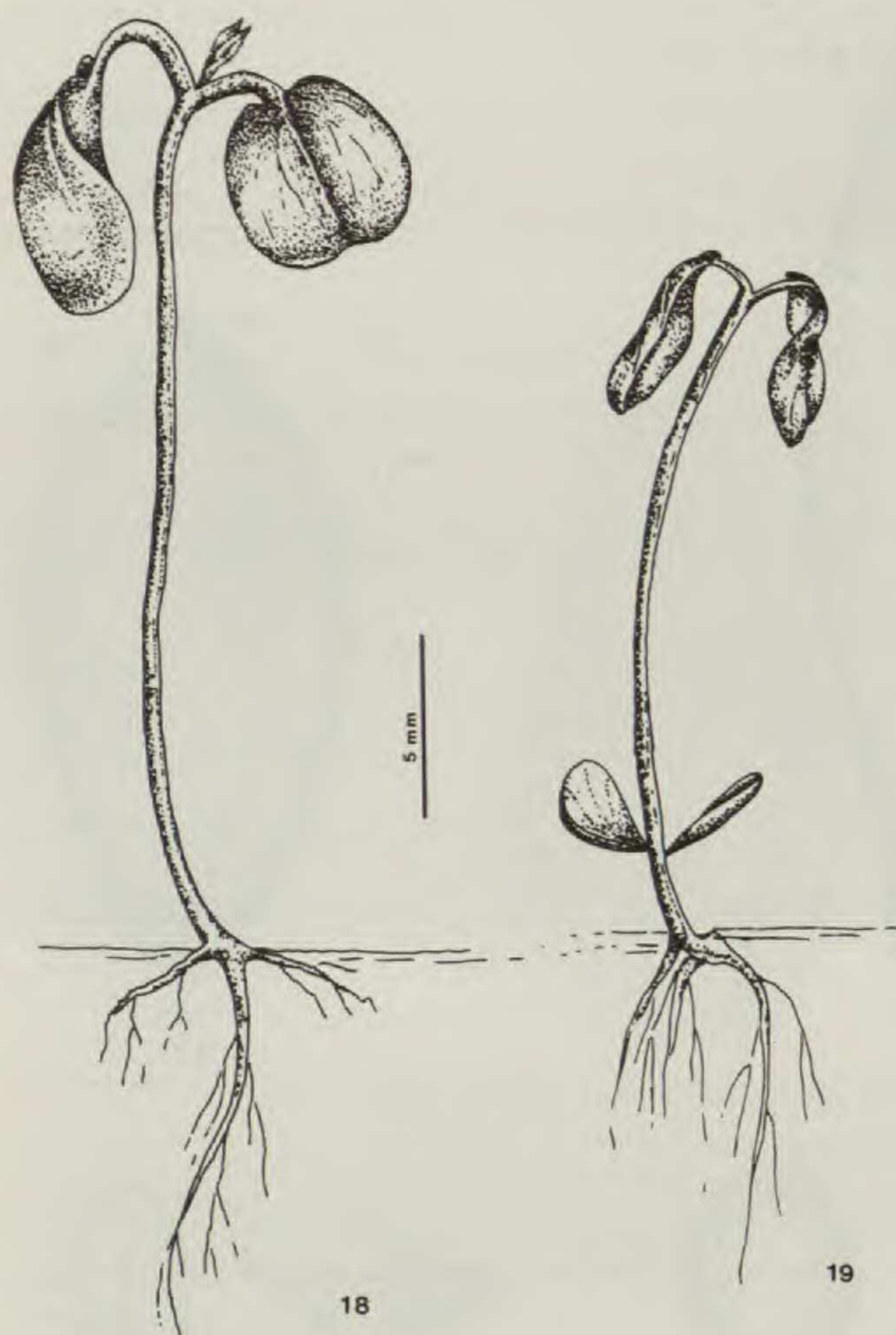
FIGURES 15-17. Capsule and seed variability in the *Aphelandra pulcherrima* complex.—15. Dorsiventrally flattened, stipitate capsule (a, frontal view; b, lateral view) and flattened seeds (c) characteristic of species of Group II: (8) *A. lingua-bovis*, (9) *A. leonardii* (figured), (10) *A. laxa*, (11) *A. campanensis*, (12) *A. hartwegiana*, and (13) *A. darienensis*.—16. Stipitate, terete capsule (a) and sub-globose seeds (b) characteristic of: (1) *A. terryae*, (2) *A. sinclairiana*, (3) *A. storkii* (figured), (4) *A. gracilis*, and (5) *A. golfodulcensis*.—17. Sub-globose, terete capsule lacking a distinct stipe (a) and sub-globose seeds (b) characteristic of (6) *A. panamensis* and (7) *A. deppeana* (figured).

the adaxial side of the corolla tube. In the *A. pulcherrima* complex, the anthers are concealed within the folded lobes of the upper lip at anthesis and emerge only when the flower is visited by a pollinator. Within the group, anther length, which ranges from 3 mm in *A. deppeana* to 10 mm in *A. hartwegiana*, is taxonomically useful, as is pollen color, which varies from cream (e.g., *A. gracilis*) to yellow (e.g., *A. leonardii*) and orange (e.g., *A. sinclairiana*).

Gynoecium. Species of *Aphelandra* characteristically have a bilocular ovary with four ovules. In the Central American group dealt with here, the ovary is uniformly green and glabrous, except that occasional individuals of *A. terryae* have red-tipped ovaries. The style is filiform and

extends to, and usually slightly beyond, the adaxial pair of anthers (Fig. 5). Most species have shallowly bilobed stigmas that may be red or pink. *Aphelandra deppeana* and *A. panamensis*, however, have oblique stigmas that appear to be hollow and are not distinctively colored.

Fruits. *Aphelandra* has explosively dehiscent capsules in which the four (or fewer) seeds are borne on membranous to woody, hook-like retinacula (Lindau, 1895; Long, 1970; Figs. 13, 14). In six of the species treated here, the capsules are clavate with a narrowed stipe below the seed-bearing portion of the fruit. They are dorsiventrally flattened and thus oval in cross-section (Fig. 15a, 15b). Five species have capsules that are stipitate and terete (Fig. 16a). In *A. deppeana*



FIGURES 18, 19. Seed germination patterns in the *Aphelandra pulcherrima* complex.—18. Epigeal germination characteristic of species of Group II: (8) *A. lingua-bovis*, (9) *A. leonardii*, (10) *A. laxa*, (11) *A. campanensis*, (12) *A. hartwegiana*, and (13) *A. darienensis*.—19. Semi-hypogeal germination, with only slight elongation of the hypocotyl, characteristic of species of Group I: (1) *A. terryae*, (2) *A. sinclairiana*, (3) *A. storkii*, (4) *A. gracilis*, (5) *A. golfodulcensis*, (6) *A. panamensis*, and (7) *A. deppeana*.

and *A. panamensis*, fruits are sub-globose, lack a distinct stipe, and are terete (Fig. 17a). All species have capsules that are elliptic in outline, except *A. sinclairiana* has capsules that are laterally narrowed between the pairs of seeds and are sinuate in outline. Capsules of most species are green when immature, but those of *A. sinclairiana* are black, and those of *A. panamensis* and *A. lingua-bovis* are dull orange-brown. Among species, capsule length ranges from 13 mm (*A. deppeana*) to 35 mm (*A. darienensis*).

Seed and seed germination patterns. As is characteristic of Acanthaceae, *Aphelandra* seeds are exalbuminous (Bremekamp, 1965). Mature seeds are various shades of brown, glabrous and orbicular to irregularly angular in outline (Figs.

15c, 16b, 17b). Of the 13 species treated here, seven have seeds that are only slightly flattened (diameter/width ratio < 2) and six have strongly flattened seeds (diameter/width ratio > 2). Relative seed width is associated with fruit morphology: sub-globose seeds occur in species with terete fruits (Figs. 16, 17), and strongly flattened seeds occur in species with similarly flattened fruits (Fig. 15).

Epigeal and semi-hypogeal germination patterns are found among the species studied here. In epigeal germination, the cotyledons are raised above the surface by elongation of the hypocotyl (Fig. 18). In semi-hypogeal germination, the cotyledons emerge from the seed but remain at the level of the substrate because no (or very little) elongation of the hypocotyl occurs (Ng, 1978; Fig. 19). Seed morphology is correlated with germination pattern: flattened seeds germinate epigeally (six species), and sub-globose seeds germinate semi-hypogeally (seven species).

SYSTEMATIC IMPLICATIONS

Comparative morphology provides evidence for the four taxonomic changes resulting from this study. *Aphelandra dukei* is considered conspecific with *A. deppeana* and three new species were described (McDade, 1982): *A. panamensis*, *A. golfodulcensis*, and *A. leonardii*. Detailed justification for these changes is provided in the taxonomic treatment. Comparative morphology also provides characters for reconstructing phylogenetic relationships among these species. The results of phylogenetic analysis are previewed here in summary form to facilitate discussion of interrelationships in subsequent sections. The Central American species treated here belong to two lineages, referred to hereafter as Groups I (species 1–7) and II (8–13) (Table 3). Species of each lineage share several derived character states (see Phylogenetic Analysis) and may be readily recognized by suites of distinguishing features (Table 3).

CHROMOSOME DATA

In the most thorough cytogenetic survey of Acanthaceae to date, Grant (1955) reported approximately 100 new chromosome counts for the family and suggested that chromosome data would be useful in studying interrelationships within the group, especially at lower taxonomic levels. Although many new counts have been reported subsequently, systematic applications

TABLE 3. Morphological characters distinguishing groups of species within the Central American members of the *Aphelandra pulcherrima* complex. NA denotes data not available.

Species	Bracteal Nectaries	Capsule	Seed	Germination Pattern	Habit
Group I					
1. <i>A. terryae</i> (TE)	Large	Terete	Sub-globose	Semi-hypogeal	Shrub
2. <i>A. sinclairiana</i> (SI)	Large	Terete	Sub-globose	Semi-hypogeal	Shrub
3. <i>A. storkii</i> (ST)	Large	Terete	Sub-globose	Semi-hypogeal	Monocaulous
4. <i>A. gracilis</i> (GR)	Large	Terete	Sub-globose	Semi-hypogeal	Shrub
5. <i>A. golfodulcensis</i> (GO)	Large	Terete	Sub-globose	Semi-hypogeal	Shrub
6. <i>A. panamensis</i> (PA)	Large	Sub-globose, terete	Sub-globose	Semi-hypogeal	Shrub
7. <i>A. deppeana</i> (DE)	Large	Sub-globose, terete	Sub-globose	Semi-hypogeal	Shrub
Group II					
8. <i>A. lingua-bovis</i> (LB)	Minute	Flattened	Flattened	Epigeal	Monocaulous
9. <i>A. leonardii</i> (LE)	Minute	Flattened	Flattened	Epigeal	Shrub
10. <i>A. laxa</i> (LA)	Minute	Flattened	Flattened	NA	Monocaulous
11. <i>A. campanensis</i> (CA)	Minute	Flattened	Flattened	Epigeal	Monocaulous
12. <i>A. hartwegiana</i> (HA)	Minute	Flattened	Flattened	Epigeal	Monocaulous
13. <i>A. darienensis</i> (DA)	Minute	Flattened	Flattened	Epigeal	Monocaulous

of cytological data are essentially lacking. The chromosome numbers reported previous to this study for four species of *Aphelandra* ($n = 14, 14, 28, 34$; Table 4) suggested that cytology might be valuable in elucidating relationships within the group treated here.

MATERIALS AND METHODS

Flower buds were collected from both field populations and greenhouse plants (grown from cuttings taken from field populations) for study of meiotic chromosomes. Root tips from cuttings and from young seedlings were used to determine mitotic chromosome numbers. Suitable cytological material was obtained from at least one locality of all species except *A. laxa*. Chromosome vouchers are deposited at DUKE. All materials were fixed in Carnoy's solution (3 absolute alcohol: 1 glacial acetic acid) for 24 hours at room temperature or for four hours at 60°C. Material not processed immediately was stored in 70% ethanol and kept refrigerated when possible.

Anthers or root tips were gently boiled for about five minutes in acetocarmine (saturated solution of carmine in 45% acetic acid). A single anther or root tip was then transferred to a drop of 45% acetic acid. The root cap was removed and the distal 1–2 mm of the meristem was excised. The root tip or anther was then placed in a small drop

of Hoyer's solution (Anderson, 1954; Beeks, 1955) on a clean slide. The tissue was gently broken apart using a dissecting needle or flat scalpel edge, a cover glass was added and pressure applied to spread and flatten the preparation.

RESULTS

The haploid number of all 12 species is 14 (Table 5). Karyotype analysis proved impossible due to the small size of the chromosomes (2–3 μm) and their tendency to clump in metaphase cells. The same difficulties were reported by Grant (1955) in his work with the closely related tribe Acantheae.

The previously reported meiotic count of $n =$

TABLE 4. Published reports of chromosome numbers of species of *Aphelandra*.

Species	n	Source
<i>A. aurantiaca</i>	14	Takizawa, 1957
<i>A. chamissoniana</i>	14	Takizawa, 1957
<i>A. fulgens</i> (= <i>A. deppeana</i>) ^a	28	Pal, 1964
<i>A. cristata</i> (= <i>A. tetragona</i>) ^b	34	Narayanan, 1951

^a Species included in this study.
^b South American member of the *A. pulcherrima* complex.

TABLE 5. Chromosome numbers of Central American species of the *Aphelandra pulcherrima* complex. NA denotes data not available.

Species	<i>n</i>	<i>2n</i>	Voucher
1. <i>A. terryae</i> Standley	NA	28	Panama. Darién: along Río Pirre ca. 10 km S of El Real, <i>McDade</i> 431.
2. <i>A. sinclairiana</i> Nees	14	NA	Panama. Colón: ca. 14 km from Colón along hwy. to Panamá, <i>McDade</i> 384.
	14	NA	Panama. Colón: along Pipeline Rd., <i>McDade</i> 280.
3. <i>A. storkii</i> Leonard	14	NA	Costa Rica. Heredia: Finca La Selva, near Pto. Viejo, <i>McDade</i> 350.
4. <i>A. gracilis</i> Leonard	NA	28	Panama. Panamá: slopes of Cerro Jefe, <i>McDade</i> 420.
5. <i>A. golfodulcensis</i> McDade	14	NA	Costa Rica. Puntarenas: San Vito de Java, <i>McDade</i> 251.
	14	28	Costa Rica. Puntarenas: Corcovado National Park, <i>McDade</i> 401.
6. <i>A. panamensis</i> McDade	NA	28	Panama. Colón: Sta. Rita Ridge, ca. 7 km from hwy. between Panamá and Colón, <i>McDade</i> 388.
	14	NA	Panama. Darién: slopes of Cerro Pirre, <i>McDade</i> 428.
7. <i>A. deppeana</i> Schldl. & Cham.	NA	28	Costa Rica. Puntarenas: ca. 18 km SE of Palmar N., <i>McDade</i> 290.
8. <i>A. lingua-bovis</i> Leonard	14	NA	Costa Rica. Puntarenas: Corcovado National Park, <i>McDade</i> 402.
	NA	28	Panama. Darién: summit and upper slopes of Cerro Pirre, <i>McDade</i> 429.
9. <i>A. leonardii</i> McDade	14	28	Costa Rica. San José: Río Tarrazú near Frailes, <i>McDade</i> 310.
11. <i>A. campanensis</i> Durkee	NA	28	Costa Rica. Limón: ca. 5 km N of Bribri, <i>McDade</i> 242.
12. <i>A. hartwegiana</i> Nees ex Benth.	NA	28	Panama. Darién: along trail between El Real and Pirre, <i>McDade</i> 425.
13. <i>A. darienensis</i> Wassh.	NA	28	Panama. Darién: upper slopes of Cerro Pirre, <i>McDade</i> 430.

28 for *A. fulgens* (= *A. deppeana*) (Pal, 1964) is in conflict with my determination of $2n = 28$ for both meiotic and mitotic cells of the same species from Costa Rica. Pal does not indicate the source of the plant(s) from which the count was obtained, but the species was apparently cultivated in a botanical garden. Study of this species throughout its extensive range will be required to document and described this possible variation in chromosome number. The $2n = 68$ report for *A. tetragona* (Narayanan, 1951), a Venezuelan species belonging to the *A. pulcherrima* complex, suggests that chromosomal differentiation

has occurred at least to some extent in the South American members of the complex and that further cytological work is warranted.

Although chromosome numbers have been determined for a small proportion of *Aphelandra* species (15 of about 170), counts of $n = 14$ for representatives of three distantly related species groups [*A. aurantiaca* (Scheidw.) Lindl., *A. chamissoniana* Nees, *A. pulcherrima* group] suggest that 14 is the base number of the genus. This same number has been reported for species belonging to most other tribes within Acanthaceae (Grant, 1955).

POLLEN

The diversity of pollen morphology in Acanthaceae is well-known (Erdtman, 1966) and its taxonomic importance has long been emphasized (Radlkofer, 1883; Lindau, 1895; Bremekamp, 1944; Raj, 1961). Although the results of a somewhat restricted survey of pollen morphology served as the basis of Lindau's (1895) classification of the family at the suprageneric level, more recent and complete studies using both light and electron microscopy have revealed considerable variation within Lindau's supposedly uniform groupings (Bremekamp, 1944; Raj, 1961; Gibson, 1972; Wasshausen, 1975). To assess accurately the systematic value of pollen morphology at higher taxonomic levels, knowledge of the infrageneric range of pollen variability is necessary. Unfortunately, complete palynological surveys have been made of only a few small genera of Acanthaceae. Partial surveys of several large genera have indicated extensive infrageneric variability (e.g., *Aphelandra*: Wasshausen, 1975; *Justicia*: Raj, 1961; *Ruellia*: Chaudal, 1966).

Variability in pollen size among taxa in Acanthaceae has received little systematic attention. Even among species with morphologically indistinguishable pollen, significant differences in grain size may exist. Pollen size is readily determined and is commonly reported in palynological descriptions.

In an SEM survey of pollen of 60 species of *Aphelandra*, Wasshausen (1975) found considerable diversity in shape (spheroidal to prolate) and sculpturing (verrucose, reticulate, psilate). Although indicating that pollen characters should be useful in classification of *Aphelandra* at the species level, Wasshausen found that evidence from pollen analysis conflicted with his interpretation of the affinities of several species based on morphological studies. Resolution of these possible discordances will require thorough analysis of the relationships within *Aphelandra*, as well as a complete palynological survey of the genus. For the 13 species treated here, analysis of pollen size, shape, and ultrasculpturing using both light and scanning electron microscopy was conducted.

MATERIALS AND METHODS

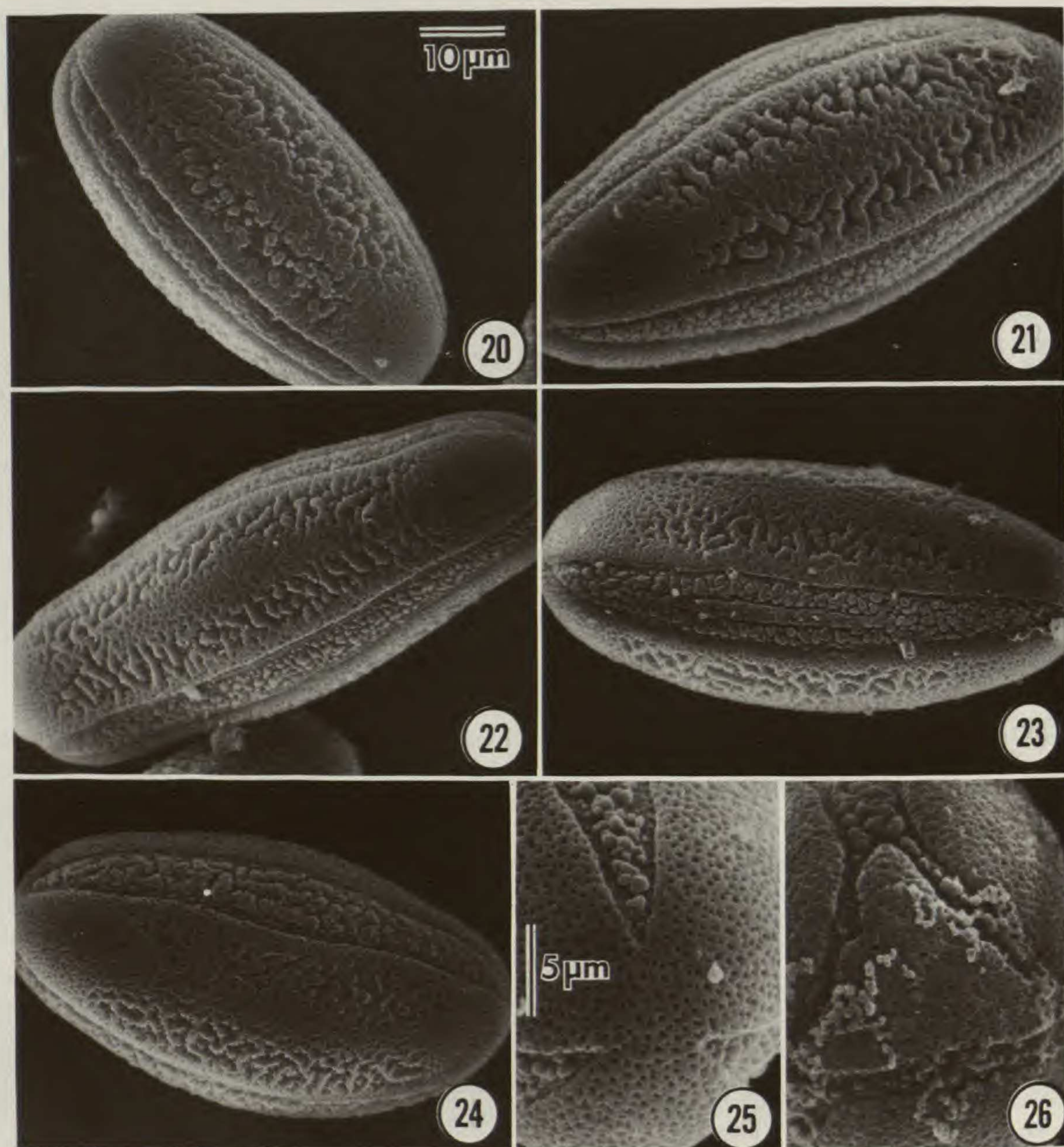
For scanning electron microscopic study (SEM), pollen was obtained from two or more plants

from each of one to five populations that spanned the geographic range of each species (Appendix B). Anthers were collected from field and greenhouse plants from flower buds one to three days prior to anthesis and fixed initially in FAA (formalin:acetic acid:alcohol). Fresh or fixed pollen of *A. laxa* was not available and thus dried anthers were removed from herbarium specimens and rehydrated for 24 hours in Aerosol OT solution. Following a dehydration series through 100% ethanol to 100% freon, the anthers were dried using carbon dioxide as a transitional fluid in a BOMAR SPC-900/EX critical point dryer. To minimize charging, a small piece of glass coated with polyvinyl chloride (in methyl ethyl ketone solution) was attached to the stub surface using low resistance cement. Pollen grains were extracted by slicing a dried anther and gently tapping it over a prepared stub. Stubs were then coated with a 250 angstrom layer of gold-palladium using a sputter coater. The samples were viewed and photomicrographs taken using a JEOL JSM-T20 scanning electron microscope.

Pollen samples to be measured for size analysis were collected from several sources including dried herbarium specimens, field populations, and greenhouse plants (Appendix B). One to seven localities from throughout the range of each species were sampled. Fresh specimens were fixed initially in FAA and stored for varying lengths of time. Both dried and FAA-fixed anthers were acetolyzed by boiling in 9:1 acetic anhydride:sulfuric acid, straining to remove anther debris, boiling in 10% KOH, and eventual storing in 70% ethanol (Livingstone, pers. comm.). Two sub-samples of at least 25 grains were taken from each sample and mounted in aniline blue in lactophenol solution. Length and width of each grain were measured under high dry magnification of $400\times$ (bright field light microscopy). These data were analyzed by Analysis of Variance (ANOVA), followed by Duncan Multiple Range a posteriori test for significant differences among species means (Sokal & Rohlf, 1969; SAS User's Guide, 1979).

RESULTS

Pollen of all 13 *Aphelandra* species studied is isopolar, radiosymmetric, tricolpate, and prolate (*A. panamensis*) to prolate (remaining 12 species). With few exceptions as noted below, there is little variability at either the individual or population level among grains of the same



FIGURES 20–26. *Aphelandra* pollen of Type I (scanning electron photomicrographs).—20. (3) *A. storkii*, McDade 350 (DUKE).—21. (1) *A. terryae*, McDade 431 (DUKE).—22. (4) *A. gracilis*, McDade 529 (DUKE).—23. (5) *A. golfodulcensis*, McDade 401 (DUKE).—24. (2) *A. sinclairiana*, McDade 389 (DUKE).—25. (3) *A. storkii*, polar view, McDade 350 (DUKE).—26. (5) *A. golfodulcensis*, polar view, McDade 251 (DUKE).

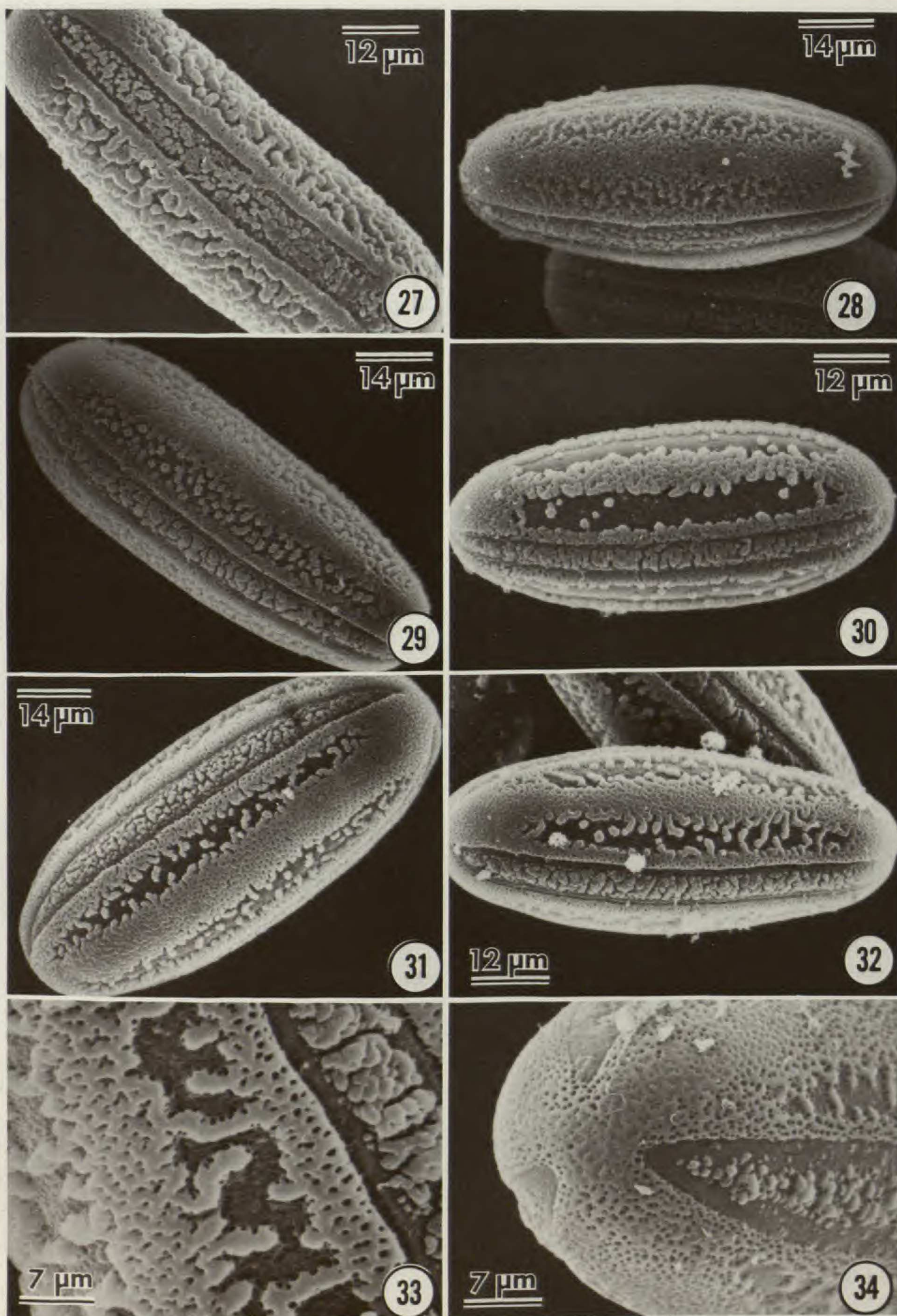
species. Three pollen types are distinguished on the basis of morphology (shape and sculpturing).

Type I (Figs. 20–26). Pollen perprolate and tapering to the poles, colpi not meeting at the poles (Fig. 25). Sculpturing gemmate to verrucose over colpi, finely reticulate elsewhere with the exception of longitudinal bands of vermiculate sculpturing along both edges of each colpus, these extending from the equator about halfway to each pole.

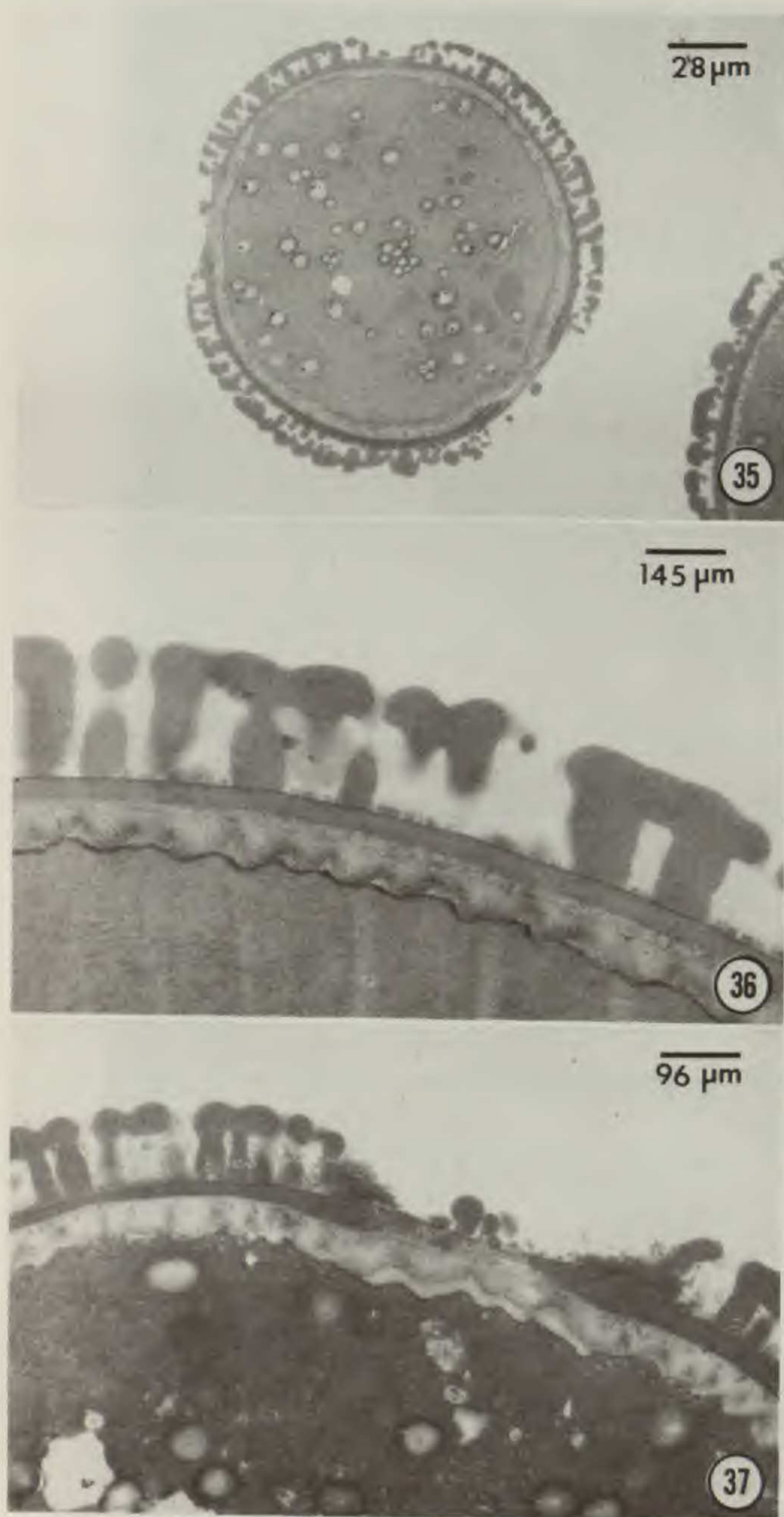
Aphelandra terryae, *A. sinclairiana*, *A. storkii*, *A. golfodulcensis*, and *A. gracilis* (species 1–5, Figs. 20–26) have pollen of Type I. Among these

species, there is little difference in pollen morphology although grain size differs markedly (see below). A few individuals of *A. golfodulcensis* show unusual colpi that bifurcate near the poles and meet, leaving a triangular shield of typical finely reticulate exine at the pole (Fig. 26).

Type II (Figs. 27–34). Grains similar to Type I in shape (perprolate and tapering to the poles) and morphology of the colpi. Exine sculpturing gemmate to verrucose over colpi, finely reticulate elsewhere, except longitudinal bands devoid of sculpturing along both edges of each colpus. These bands interlaced and bordered with regions of



FIGURES 27-34. *Aphelandra* pollen of Type II (scanning electron photomicrographs).—27. (10) *A. laxa*, Mori et al. 6854 (MO).—28. (9) *A. leonardii*, McDade 310 (DUKE).—29. (9) *A. leonardii*, McDade 432 (DUKE).—30. (11) *A. campanensis*, McDade 273 (DUKE).—31. (12) *A. hartwegiana*, McDade 425 (DUKE).—32. (13) *A. darienensis*, McDade 430 (DUKE).—33. (11) *A. campanensis*, McDade 273 (DUKE).—34. (11) *A. campanensis*, McDade 242 (DUKE).



FIGURES 35–37. Ultrastructure of *Aphelandra* pollen (transmission electron photomicrographs, preparation after Stone et al., 1979).—35. Cross-section, note three colpi with reduced exine.—36. Structure of wall, well-developed intine and exine (composed of foot-layer, columellae and tectum).—37. Reduction of wall (particularly of exine layers) over colpus. (*Aphelandra storkii*, McDade 350.)

vermiculate exine (Fig. 33) and extending from the equator approximately half the distance to each pole.

Aphelandra leonardii, *A. laxa*, *A. campanensis*, *A. hartwegiana*, and *A. darienensis* (species 9–13, Figs. 27–34) have pollen of Type II. Among these species, there are differences with respect to width of unsculptured bands (narrow in *A. leonardii* and *A. laxa*, quite broad in *A. dari-*

ensis), as well as in size (see below). Structurally, the unsculptured regions probably are the exposed foot layer of the exine, with the columellae and tectum lacking (Figs. 35–37).

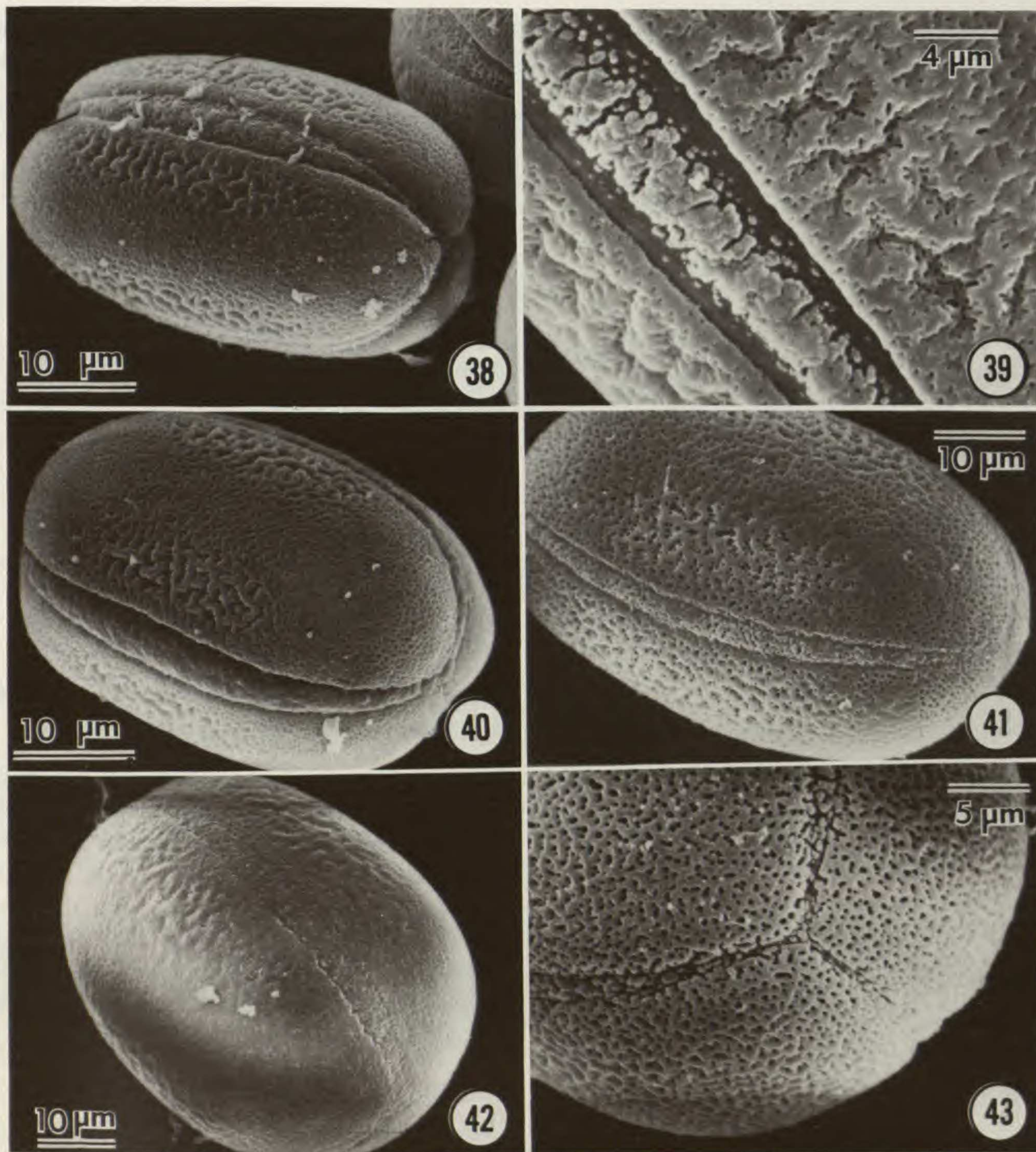
Type III (Figs. 38–43). Pollen prolate to barely perprolate, tapering very little from equator to the poles so that grains are somewhat rectangular, syntriolate (colpi meeting at the poles; Figs. 40, 43). Exine finely reticulate to vermiculate over colpi, elsewhere finely reticulate. Longitudinal bands along colpi may be quite indistinct (Fig. 42) or may be well-defined regions bearing vermiculate sculpturing (Figs. 40, 41).

Aphelandra deppeana, *A. panamensis*, and *A. lingua-bovis* (species 6–8; Figs. 38–43) have pollen of Type III. Pollen of the last species is somewhat variable among populations with respect to degree of sculpturing relief (from quite smooth, extremely finely reticulate grains with ill-defined colpi, to rather coarsely reticulate grains with vermiculate colpi; i.e., contrast Figs. 41, 42). Although grains of these species are quite similar in shape, there is significant size disparity between *A. lingua-bovis* and the other species.

Pollen grains of the 13 species range in length from 45.6 μm (*A. panamensis*) to 88.6 μm (*A. hartwegiana*), and in width from 24.8 μm (*A. deppeana*) to 40.0 μm (*A. lingua-bovis*). Analysis of variance revealed significant differences among species in both length ($F_s = 375.83$; 13,3083 df; $P < 0.00001$), and width ($F_s = 321.00$; 13,3083 df; $P < 0.0001$). Duncan Multiple Range test for differences among means permitted further resolution of these data into statistically distinguishable groups of means (Tables 6, 7). All species can be distinguished on the basis of pollen length, width, or both, with the exception of two species pairs: *A. darienensis*–*A. lingua-bovis*, and *A. golfodulcensis*–*A. sinclairiana*. When both morphology and size of pollen are considered, only *A. golfodulcensis* and *A. sinclairiana* remain indistinguishable.

SYSTEMATIC IMPLICATIONS

Pollen characters support three of four taxonomic changes made in this treatment. Pollen morphology separates *A. leonardii*, with pollen of Type II, from *A. pulcherrima* which has pollen of Type I (Figs. 44, 45). Although grains of *A. deppeana* and *A. panamensis* are not distinguishable by shape and sculpturing, pollen length and width differ (Tables 6, 7). The results of pollen



FIGURES 38–43. *Aphelandra* pollen of Type III (scanning electron photomicrographs).—38. (7) *A. deppeana*, McDade 533 (DUKE).—39. (7) *A. deppeana*, McDade 396 (DUKE).—40. (6) *A. panamensis*, McDade 428 (DUKE).—41. (8) *A. lingua-bovis*, McDade 399 (DUKE).—42. (8) *A. lingua-bovis*, McDade 380 (DUKE).—43. (8) *A. lingua-bovis*, polar view, McDade 399 (DUKE).

analysis also support the inclusion of *A. dukei* within *A. deppeana*: the grains are indistinguishable both morphologically (Figs. 46, 47) and in length and width (Tables 6, 7). However, pollen characters provide no additional basis for the recognition of *A. golfodulcensis* as distinct from *A. sinclairiana*.

Pollen morphology also provides evidence for the recognition of interrelated groups among these 13 species. With the exception of *A. lingua-bovis*, the species of Group II (9–13) share pollen of

Type II. Species 1–5 (Group I, excepting *A. deppeana* and *A. panamensis*) have Type I pollen. Of the three remaining species sharing pollen Type III, *A. deppeana* and *A. panamensis* are close relatives. The relationship of these two with *A. lingua-bovis* is less clear and is discussed in more detail subsequently.

Preliminary surveys of additional species of *Aphelandra* (Wasshausen, 1975; McDade, unpubl. data) suggest that pollen morphology, together with size analysis, has considerable sys-

TABLE 6. Pollen length variability among Central American species of the *Aphelandra pulcherrima* complex.

Species	N (Populations, Grains)	Pollen Length ^a (Mean ± 1 s.d.)	Pollen Type ^b
12. <i>A. hartwegiana</i>	4, 162	88.6 ± 10.59	II
10. <i>A. laxa</i>	1, 50	82.1 ± 4.36	II
13. <i>A. darienensis</i>	1, 65	80.9 ± 3.74	II
11. <i>A. campanensis</i>	4, 407	79.0 ± 9.04	II
9. <i>A. leonardii</i>	7, 344	78.7 ± 7.20	II
8. <i>A. lingua-bovis</i>	6, 273	78.5 ± 9.48	III
4. <i>A. gracilis</i>	5, 212	74.7 ± 7.44	I
1. <i>A. terryae</i>	5, 167	74.1 ± 10.53	I
5. <i>A. golfodulcensis</i>	7, 361	70.6 ± 7.94	I
2. <i>A. sinclairiana</i>	8, 451	69.5 ± 8.43	I
3. <i>A. storkii</i>	1, 93	61.1 ± 3.49	I
<i>A. "dukei"</i>	1, 34	49.8 ± 2.70	III
7. <i>A. deppeana</i>	7, 239	49.7 ± 7.22	III
6. <i>A. panamensis</i>	3, 138	45.6 ± 8.12	III

^a Bars connect means not significantly different (*P* > 0.05).

^b See text.

tematic potential. At least three additional morphological types are recognizable that may clarify relationships within the large and heterogeneous genus.

REPRODUCTIVE BIOLOGY

Field investigations were undertaken to characterize the floral biology of the Central American species of the *Aphelandra pulcherrima* complex (McDade, 1980). Aspects of particular systematic significance discussed here are sea-

sonality and phenology of flowering, pollinator relationships, and seed dispersal.

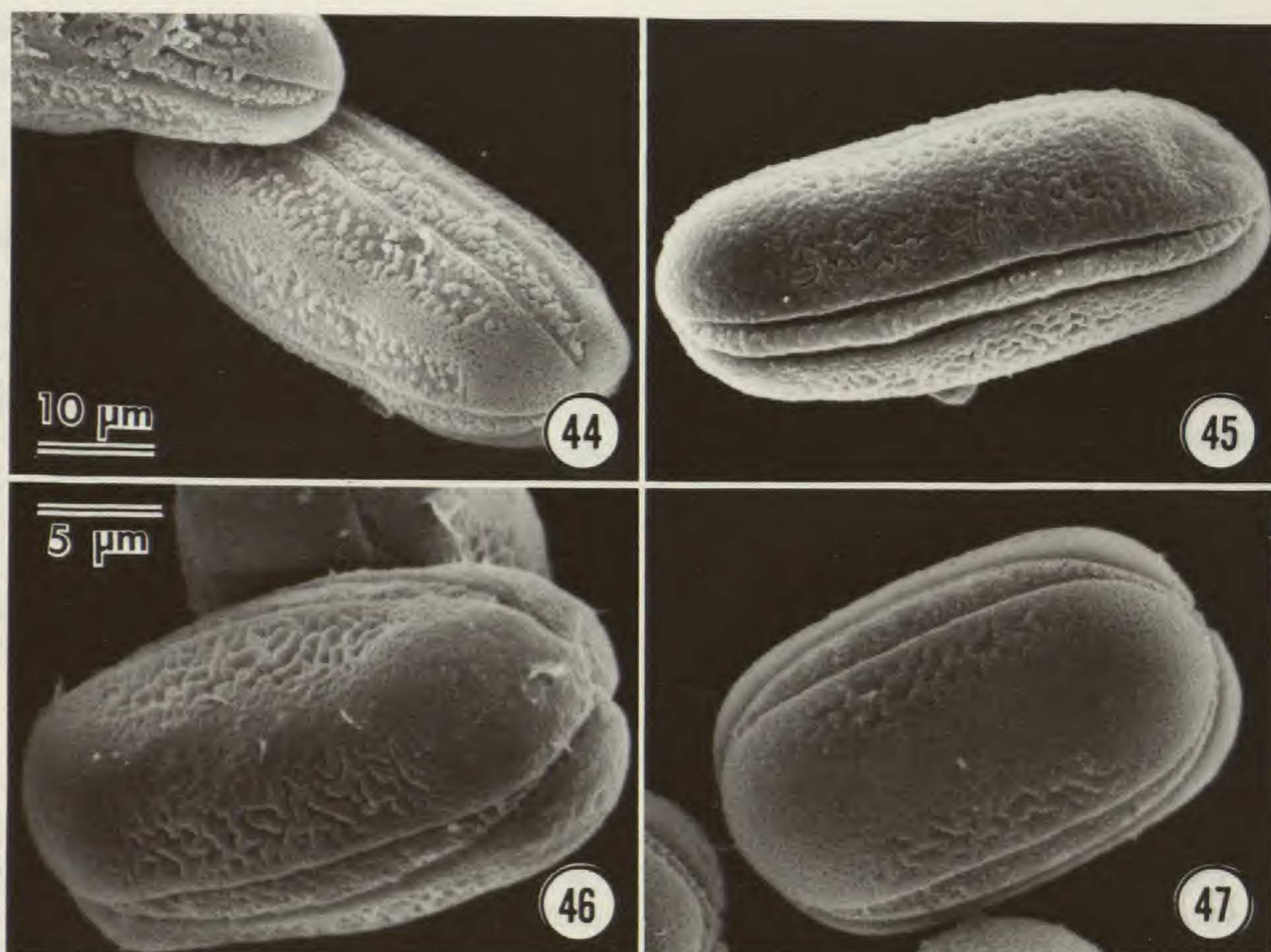
Seasonality and phenology. Flowering seasonality was determined for 12 species of *Aphelandra* over the course of 18 months of field work, augmented by study of herbarium specimens. Four species flower during the Central American dry season (late Dec. through March or April), and eight flower during the wet season (April or May to Dec.) (Table 8). At least five of the wet season flowering species (*A. panamensis*, *A. stor-*

TABLE 7. Pollen width variability among Central American species of the *Aphelandra pulcherrima* complex.

Species	N (Populations, Grains)	Pollen Width ^a (Mean ± 1 s.d.)	Pollen Type ^b
8. <i>A. lingua-bovis</i>	6, 273	40.0 ± 5.76	III
13. <i>A. darienensis</i>	1, 65	38.7 ± 2.72	II
12. <i>A. hartwegiana</i>	4, 162	38.1 ± 4.79	II
11. <i>A. campanensis</i>	4, 407	35.4 ± 5.42	II
9. <i>A. leonardii</i>	7, 344	32.1 ± 4.24	II
10. <i>A. laxa</i>	1, 50	31.2 ± 2.54	II
4. <i>A. gracilis</i>	5, 212	29.7 ± 4.08	I
3. <i>A. storkii</i>	1, 93	29.6 ± 2.84	I
2. <i>A. sinclairiana</i>	8, 451	28.0 ± 7.96	I
1. <i>A. terryae</i>	5, 168	27.1 ± 3.31	I
5. <i>A. golfodulcensis</i>	7, 361	27.1 ± 3.16	I
6. <i>A. panamensis</i>	3, 138	27.1 ± 3.08	III
7. <i>A. deppeana</i>	7, 239	24.8 ± 3.01	III
<i>A. "dukei"</i>	1, 34	22.2 ± 1.43	III

^a Bars connect means not significantly different (*P* > 0.05).

^b See text.



FIGURES 44–47. Pollen morphology of two taxonomically difficult pairs of *Aphelandra* species (scanning electron photomicrographs).—44. (9) *A. leonardii*, McDade 432 (DUKE).—45. *A. pulcherrima*, Blum 3523 (US).—46. *A. dukei*, Duke 14397 (US).—47. (7) *A. deppeana*, McDade 290 (DUKE).

kii, *A. lingua-bovis*, *A. leonardii*, and *A. hartwegiana*) mature fruits during the following dry season. This fruiting pattern may have adaptive value since *Aphelandra* fruits must desiccate before dehiscence and seed dispersal can occur.

Field and greenhouse observations indicate that flowers open at or shortly after dawn and fall in the late afternoon or night of the same day. Release of pollen coincides with floral anthesis; by late afternoon, the anthers are empty and discolored. Controlled pollinations of greenhouse plants indicate that the stigma is receptive immediately following anthesis and that there is no temporal separation of male and female phases. There is, however, considerable spatial separation: the stigmas of all species are exerted 3–10 mm beyond the anthers. This separation effectively prevents autogamy (McDade, 1980).

Aphelandra flowers secrete nectar beginning just prior to anthesis and continuing until late afternoon (McDade, 1980; McDade & Kinsman, 1980). Sugar concentration in the nectar of six species ranged from 24% to 36% (McDade, 1980). Flowers of the species treated here are odorless, at least to human sensitivities. However, inflo-

rescences of *A. sinclairiana* have a sweet, citrus-like aroma.

Flower visitors. Observations were made to identify animals that consume the floral resources (nectar and/or pollen) of *Aphelandra*, and to characterize the behavior of each species visiting the flowers. A visit was defined as actual physical contact of the animal with at least one flower. In a “legitimate” visit, an animal gained access to the nectar through the natural opening at the distal end of the corolla tube. All other means of extracting nectar or pollen were considered “illegitimate.” Observation periods of 45 minutes or longer were scheduled to cover daylight hours as fully as possible, and were conducted at 14 localities of ten species (Table 9; Appendix C). Data were not obtained for *A. darriensis*, *A. terryae*, or *A. laxa*.

A summary of the observed animal visitors is presented by species of *Aphelandra* in Table 9. Flowers of all species observed were pollinated by hummingbirds. The complex and extremely consistent floral morphology and phenology of all 13 species treated here suggests that the three

TABLE 8. Flowering seasonality of Central American species of the *Aphelandra pulcherrima* complex.

Wet Season	Dry Season
3. <i>A. storkii</i>	1. <i>A. terryae</i>
6. <i>A. panamensis</i>	2. <i>A. sinclairiana</i>
7. <i>A. deppeana</i>	4. <i>A. gracilis</i>
8. <i>A. lingua-bovis</i>	5. <i>A. golfodulcensis</i>
9. <i>A. leonardii</i>	
11. <i>A. campanensis</i>	
12. <i>A. hartwegiana</i>	
13. <i>A. darienensis</i>	

species not studied in the field have the same pollinators. The distinctive morphology of the upper corolla lip restricts potential pollinators to animals with mouth parts sufficiently deep to open the upper lip and bring the anthers and stigma into contact with the visitor's body. Animals with narrow mouth parts (e.g., Lepidoptera, Hymenoptera) would never contact the functional floral organs and thus could not be effective pollinators.

With two exceptions, flowers were pollinated virtually exclusively by two species of large hermit hummingbirds (Trochilidae: Phaethorninae): *Phaethornis superciliosus* (long-tailed hermit) and *P. guy* (green hermit). These birds range from central Mexico to northern Bolivia and Amazonian Brazil (*P. superciliosus*), and from Costa Rica to northern Venezuela and southern Peru (*P. guy*). *Phaethornis superciliosus* occurs from sea level to about 900 m, and *P. guy* replaces it at mid-elevations (to about 1,700 m). Flowers of *A. lingua-bovis* and *A. campanensis*, which range from the lowlands to over 1,000 m, are pollinated by both birds. Most species, however, have more restricted elevational distributions and have only one pollinator. There is a close correspondence between the corolla tube length (35–45 mm above basal constriction) and curvature, and the bill length (35–44 mm) and curvature of both species of *Phaethornis*. Thus, these birds are able to gain access to nectar near the base of the corolla and to effect pollination in a "legitimate" visit (i.e., hovering in front of the flower and inserting the bill at the mouth of the corolla tube, causing the pocket-like corolla lip to open, thus bringing the anthers and stigma into contact with the bird's head). Three additional lines of evidence suggest that these birds are effective pollinators: (1) pollen of *A. storkii* was removed from the crown feathers of several individuals of *P. superciliosus* at La Selva, Costa

Rica; (2) hummingbirds that visit *Aphelandra* usually have a clearly visible crown patch of pollen following flower probing; and (3) all of the species observed in the field set fruit and seed (McDade, 1980).

In addition to close morphological correspondence between flowers of *Aphelandra* and their pollinators, there is notable coincidence between hermit foraging behavior and the spatial distribution of the plants. In minimally disturbed areas, plants occur as isolated individuals or small clumps in natural openings of the forest canopy (e.g., tree falls, stream edges). Similarly, most hermit hummingbirds forage on established circuits (traplines) among dispersed individuals and small clumps of species with distinctive floral morphologies (Skutch, 1964; Snow & Snow, 1972; Stiles, 1975, 1977; Feinsinger & Colwell, 1978). My observations agree with this view of hermit foraging: there was none of the aggressive behavior associated with defense of territories by other hummingbird species (Stiles, 1975, 1977; Feinsinger, 1976). Except for brief periods of resting and preening, hermit pollinators moved away from plants immediately after visiting the open flowers. Within a patch or individual, pollinators generally visited every accessible flower unless the patch was extremely large or the foraging bird was disturbed in some way.

Aphelandra leonardii was the only long-flowered species not visited by one or both species of large *Phaethornis* hummingbirds. Flowers of this species at Frailes, Costa Rica were visited by the violet sabrewing (*Campylopterus hemileucurus*). Individuals of this species have bills that coincide morphologically with size and structure of flowers of *Aphelandra*. Ridgely (1976) and Feinsinger (1976) have characterized this bird's foraging behavior as hermit-like. It is clear that pollen was transferred effectively at this site because high levels of fruit and seed set were observed (McDade, 1980).

Aphelandra deppeana, with corollas only 36–42 mm long, was pollinated by a different group of hummingbirds (Table 9). Although euglossine bees have been reported to pollinate flowers of this species (Deuth, 1977), hummingbirds of the subfamily Trochilinae were the most frequent flower visitors at my study site. Territorial behavior by male blue-tailed hummingbirds (*Amazilia cyanura*) foraging in large patches of *A. deppeana* was observed. More sporadic, non-territorial feeding by members of both this species and *A. rutila* (cinnamon hummingbird) occurred at small clumps and isolated plants. Bill length

TABLE 9. Animal visitors to flowers of Central American species of the *Aphelandra pulcherrima* complex. NA denotes data not available.

Species and Location (Total Hr. Observed)	Legitimate Visitors (Pollinators)	Illegitimate Visitors		
		Nectar Robbers		Pollen Robbers
		Birds	Insects	
1. <i>A. terryae</i>	NA	NA	NA	NA
2. <i>A. sinclairiana</i> Colón (23)	<i>Phaethornis</i> <i>superciliosus</i>	<i>P. longuemareus</i> <i>Chalybura buffoni</i> ^a	<i>Trigona</i> sp. <i>Xylocopa</i> sp.	<i>Trigona</i> sp.
3. <i>A. storkii</i> Pto. Viejo (31.5)	<i>P. superciliosus</i>	<i>P. longuemareus</i>	<i>Trigona</i> sp.	<i>Trigona</i> sp.
4. <i>A. gracilis</i> El Valle (3)	<i>P. guy</i>	<i>P. longuemareus</i>	—	—
5. <i>A. golfodulcensis</i> Corcovado (12)	<i>P. superciliosus</i>	<i>P. longuemareus</i> ^a <i>Heliothrix barroti</i> ^a <i>Thalurania furcata</i> <i>Amazilia tzacatl</i> <i>Coereba flaveola</i>	<i>Trigona</i> sp. <i>Xylocopa</i> sp.	<i>Trigona</i> sp.
San Vito (11.25)	<i>P. guy</i>	<i>P. longuemareus</i>	—	—
6. <i>A. panamensis</i> Cerro Pirre (2.5)	<i>P. guy</i>	<i>P. longuemareus</i>	—	—
7. <i>A. deppeana</i> Cañas (11.75)	<i>A. cyanura</i> <i>A. rutila</i>	<i>A. cyanura</i> <i>Chlorostilbon canivetii</i>	—	<i>Trigona</i> sp.
8. <i>A. lingua-bovis</i> Corcovado (6.75)	<i>P. superciliosus</i>	<i>P. longuemareus</i> <i>C. flaveola</i>	—	—
San Vito (8.75)	<i>P. guy</i>	<i>P. longuemareus</i>	—	—
9. <i>A. leonardii</i> Frailes (1.5)	<i>Campylopterus</i> <i>hemileucurus</i>	—	—	—
10. <i>A. laxa</i>	NA	NA	NA	NA
11. <i>A. campanensis</i> El Valle (4.75)	<i>P. guy</i>	<i>P. longuemareus</i>	—	—
El Copé (1)	<i>P. guy</i>	—	—	—
12. <i>A. hartwegiana</i> Río Pirre (4)	<i>P. superciliosus</i>	—	—	—
13. <i>A. darienensis</i>	NA	NA	NA	NA

^a Primarily robbing species occasionally observed to visit legitimately.

of both species (17–23 mm) corresponds to corolla tube length in *A. deppeana* (22–24 mm above basal constriction). Observation of pollen on the crowns of foraging individuals, as well as high fruit and seed set (McDade, 1980), indicates that these birds are effective pollinators.

In addition to visits by pollinating hummingbirds, several other sorts of flower visits were observed (Table 9). Eight species were visited by birds with short bills that pierced or ripped holes near the base of the corolla tube to gain access to nectar. Birds visiting in this manner never contact the anthers or stigma and are not pollinators. Flowers of four species were also visited

by bees, particularly *Trigona* spp. (Apidae: Meliponinae). These bees most frequently collected pollen from flowers, but also took nectar from two species (*A. golfodulcensis* and *A. storkii*). Individual bees typically settled on the upper corolla lip, chewed through the folded corolla lobes, and collected pollen from the concealed anthers. Because the stigma is exerted several mm beyond the anthers, bees are unlikely to contact the stigma while gathering pollen. In fact, these bees frequently severely damaged or severed the style at the level of the anthers, precluding seed set. *Trigona*, as well as occasional carpenter bees (Anthophoridae: Xylocopinae, *Xylocopa* sp.) ex-

TABLE 10. Comparison of seed set from inter- and intrapopulation crosses of *Aphelandra* species.

Species	Inter	Intra	t_s	df
5. <i>A. golfodulcensis</i>	0.590	0.490	3.478 ^a	7
6. <i>A. panamensis</i>	0.448	0.210	257.089 ^b	1
7. <i>A. deppeana</i>	0.636	0.535	9.528 ^b	9
8. <i>A. lingua-bovis</i>	0.109	0.223	38.776 ^b	3
9. <i>A. leonardii</i>	0.461	0.614	182.143 ^b	5

^a $P < 0.01$.^b $P < 0.001$.

tracted nectar through holes made near the base of the corolla tube.

Because they affect nectar and pollen resources available for pollinators, these non-pollinating bird and insect visitors are an important component of the floral biology of some populations of *Aphelandra* (McDade & Kinsman, 1980). The extent of their impact in terms of fruit and seed set, however, remains to be fully determined.

Seed dispersal. Seeds of *Aphelandra* are dispersed by explosive dehiscence of the capsules. The two woody lateral ribs are held together at the apex in immature fruits by hygroscopic cells. As capsules mature and dry, this tissue ruptures and dehiscence occurs as the ribs spring apart from the apex, arching outward from the rachis (Bremekamp, 1965; Sell, 1969; Figs. 13, 14). The retinacula, two of which are attached to each woody rib of the capsule, each hold one seed and insure that the seeds are propelled away from the parent plant rather than falling directly to the ground. Dispersal distances vary depending upon position of the fruit and plant, and surrounding vegetation. Limited observations of *A. sinclairiana* in Panama indicate that seeds can be thrown more than 10 m from the parent plant.

SYSTEMATIC IMPLICATIONS

Differences in flowering seasonality are an important isolating mechanism between several closely related pairs of *Aphelandra* species (Table 8). In addition, pollinator relationships of *A. deppeana* and *A. panamensis* provide support for recognizing them as distinct species. They are morphologically distinct, elevationally isolated and are pollinated by different species of hummingbirds (Table 9). These data indicate, however, that diversification of floral morphology and phenology in conjunction with pollination by different animals has not been a major feature in the radiation of this group of *Aphelandra*. Oth-

er factors must have spurred speciation and the subsequent evolution of isolating mechanisms in this group.

INTERPOPULATION CROSSES

Perhaps the most serious operational difficulty in applying the biological species concept is that of demonstrating reproductive continuity among the individuals and populations of a species. Even with plants that are readily cultivated and hand-pollinated, the logistics of carrying out the necessary crosses are prohibitive. Conducting interpopulation crosses to test for reproductive continuity within putative species must be regarded as sampling, and the results taken as evidence for or against, but not proving, potential reproductive continuity within species.

MATERIALS AND METHODS

Plants were grown in the greenhouse from cuttings or seeds taken from field populations. Crosses between sites were carried out for all species for which individuals from more than one population were available (Appendix C). Hand pollinations were made between 0730 and 0900 E.S.T., by placing an excess of pollen on the stigma of the ovulate parent. No emasculations were performed because selfing is prevented by exertion of the stigma well beyond the anthers at anthesis. The floral bracts subtending all treated flowers were color-coded using acrylic paints and observed until just prior to dehiscence of fruits or until failure to set fruit was apparent. Any inflorescence that did not set fruit, as well as distal portions of inflorescences beyond fully formed fruits, were not included in the analysis because the cause of failure to fruit was not known. Fruits were collected as they began to desiccate, opened, and the number of fully filled seeds counted. At least 50 interpopulation pollinations were attempted between plants from each pair of sites.

Fruit set from each cross was calculated as the proportion of treated flowers that produced fruits. Seed set per fruit was expressed as a fraction of the maximum of four. These two indices were multiplied to yield percent seed set; that is, the proportion of ovules in each cross that developed into mature seeds.

RESULTS

Seed set from interpopulation crosses involving five species is compared with seed set data

TABLE 11. Crossability indices between Central American species of the *Aphelandra pulcherrima* complex. The larger of the paired indices from reciprocal crosses is presented as the most conservative estimate of degree of relationship. The full matrix is presented as Appendix D. NA denotes data not available. Species numbers and abbreviations as in Table 2.

Species	1. TE	2. SI	3. ST	4. GR	5. GO	6. PA	7. DE	8. LB	9. LE	11. CA	12. HA
2. SI	0.66										
3. ST	0.59	0.39									
4. GR	0.59	NA	0.62								
5. GO	0.86	0.98	0.51	0.51							
6. PA	0.80	0.99	0.58	0.37	0.64						
7. DE	0.11	0.13	0.29	0.05	0.17	0.89					
8. LB	0.03	0.07	0	0.45	0.04	0	0.08				
9. LE	0.11	0.16	0.12	0.49	0.27	0.90	0.15	0.12			
11. CA	NA	NA	0	0	0	0	0.07	0	0.17		
12. HA	NA	NA	0.03	NA	0	0	0	0	0.26	0.04	
13. DA	0.07	0.01	0	NA	0.03	0	0	0	0.39	NA	NA

from intrapopulation crosses [representing means of at least 100 attempted pollinations for each species (McDade, 1980)] in Table 10. Interpopulation crosses of *A. golfodulcensis*, *A. panamensis*, and *A. deppeana* produced significantly more seeds than did intrapopulation crosses. The reverse occurred in *A. lingua-bovis* and *A. leonardii*. In these last two species, however, seed set from interpopulation crosses was higher than from the most fertile interspecific pollinations (Appendix D).

These data provide no evidence that there are reproductive barriers between plants from different sites of the species tested. In the form of step-wise exchange of genes through both pollen flow and dispersal events, this lack of reproductive barriers may result in reproductive continuity within these species.

ARTIFICIAL HYBRIDIZATIONS

MATERIALS AND METHODS

Interspecific pollinations were carried out with all species treated here except *A. laxa*, using greenhouse grown plants from field populations. Three to eight individuals from one to three populations of each species were used in the artificial hybridizations. Except when the number of flowers and overlapping flowering periods were limiting, at least 50 crosses of each possible combination were attempted. Controlled pollinations were carried out as described above for interpopulation crosses. Hybrid seeds were germinated on filter paper and formed vigorous, rapidly growing seedlings. Representative seedlings of each successful cross were cultivated in the greenhouse for use in future studies.

Crossability indices for each cross attempted were calculated from percent seed set from each cross. For each ovulate species, percent seed set from interspecific crosses was divided by seed set from out-crosses within that species (McDade, 1980). This was done to avoid errors in comparing results among species due to differences in gamete viability, appropriate pollination conditions, etc. Crossability indices (CIs) thus can range from zero (for crosses yielding no seeds) to greater than one (if seed set from an artificial hybridization exceeds seed set from intrapopulation crosses).

RESULTS

Crossability indices for each cross attempted are presented in Appendix D. Considerable disparity exists between indices for some species pairs, depending upon which species was the ovulate parent. For instance, in the cross *A. panamensis* ♀ × *A. sinclairiana* ♂, seed set was 0.986, whereas in the reciprocal cross, seed set was only 0.042. Although there is a significant correlation ($r = 0.313$, 90 df, $P < 0.01$) between reciprocal crossabilities for each species pair, the disparity between indices is apparent, particularly when one cross of a reciprocal pair yielded very high seed set. Many factors beyond degree of relationship can influence seed set from experimental hybridizations (e.g., interspecific and intraspecific incompatibility barriers, pollen germinability, pollen tube growth, and harmonious growth and development of the hybrid embryo within the ovary). These may vary markedly in their influence on the success of hybridizations depending on whether a species is used as the ovule or pollen parent (Ornduff,

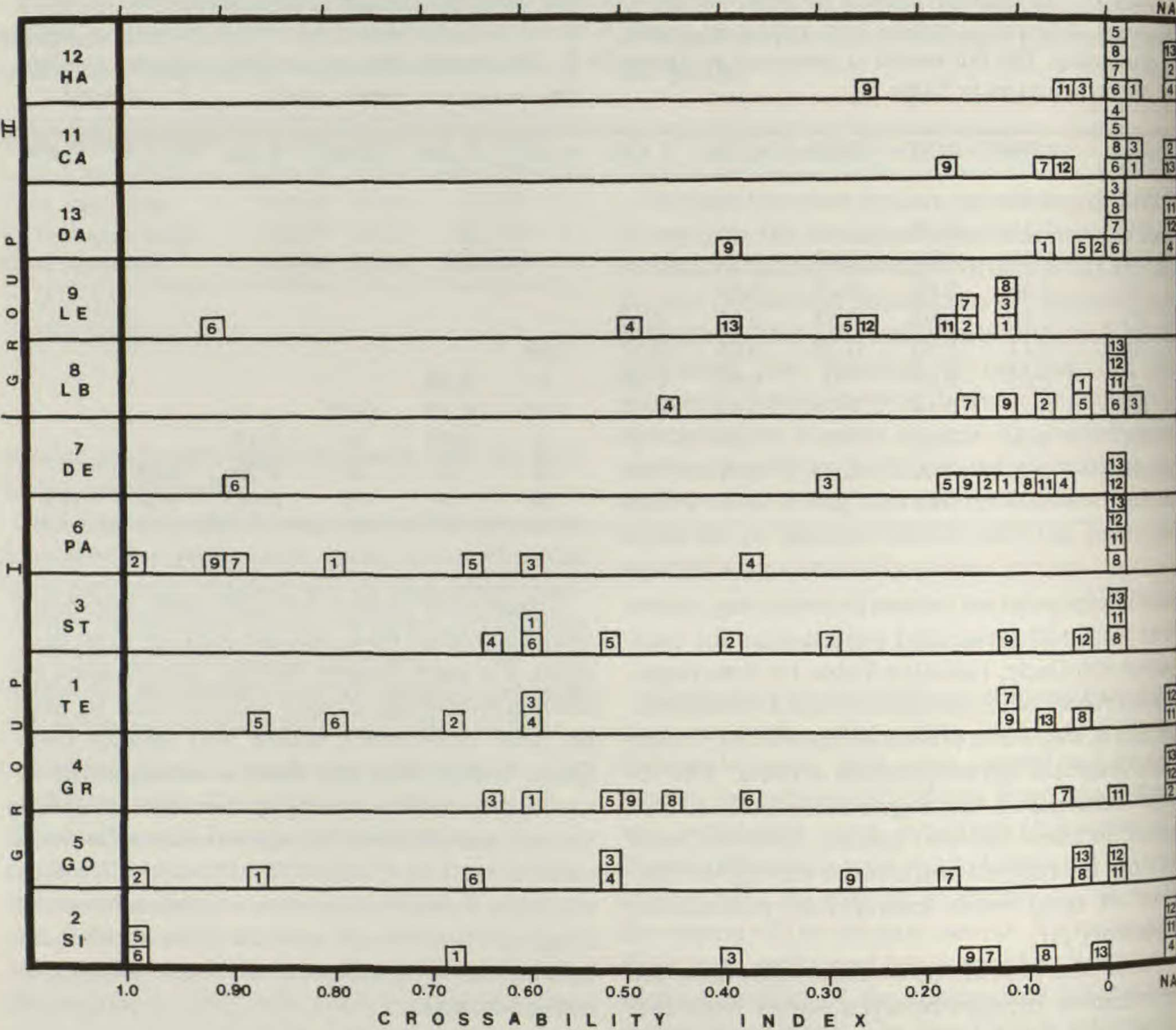


FIGURE 48. Frequency distribution table of crossability indices for 12 Central American species of the *Aphelandra pulcherrima* complex. Species are arranged in rows so that those crossing most readily are proximate. Each square is labelled with the appropriate species identification number. Data not available (NA) are indicated at the far right.

1969). For example, Lloyd (1965) crossed races of *Leavenworthia* and found that seed set was higher when the staminate parent was self-incompatible and the ovulate parent self-compatible, than when the reciprocal cross was made. The goal of this study was to obtain estimates of the degree of relationship among the species of *Aphelandra* treated here. During the evolution of these species from a common ancestor, crossability has decreased from full interfertility to various degrees of incompatibility between each pair of species. The larger of the reciprocal CIs for each species pair thus represents the most conservative estimate of relationship. The smaller index may be a product of various aspects of incompatibility beyond degree of relationship, as described above, and would over-estimate di-

vergence. The larger index for each species pair is, therefore, used in all further analyses (Table 11). Crossability indices are presented in tabular and diagrammatic form as recommended by McDade and Lundberg (1982). The frequency distribution of crossability indices (Fig. 48) shows that, with the exception of a very high crossability between species 9 (*A. leonardii*) and 6 (*A. panamensis*), all of the CIs above 0.50 are among species 1–7 (Group I, Table 3). Crossabilities among species 8–13 (Group II), and between these and species 1–7 are mostly less than 0.20. Summarization of the crossability data by group (Fig. 49) emphasizes this pattern. Species 7 (*A. deppeana*) is apparently isolated within Group I. Although species 6 and 7 are highly interfertile

(CI = 0.89), of the CIs among species 1–7, all of those below 0.30 have species 7 as one member of the pair. Species 9 (*A. leonardii*) appears to be intermediate between the two groups. Of four crossability indices above 0.20, three involve species 9, as do six of seven CIs above 0.11.

Crossability maps, representing the best two dimensional configuration of species based on the matrix of crossability indices, were constructed using Multidimensional Scaling (Kruskal & Wish, 1978; McDade & Lundberg, 1982; Fig. 50). The locations and relative proximities of species on the map are indicative of their interrelationships based upon the results of artificial hybridizations. Subsequent maps display connections between species that cross at or above five selected crossability levels (Fig. 51–55). Crossability mapping emphasizes the close relationships among species 1–6 of Group I (*A. terryae*, *A. sinclairiana*, *A. storkii*, *A. gracilis*, *A. golfodulcensis*, *A. panamensis*). Species 7 (*A. deppeana*) is closely related to species 6 (*A. panamensis*), but is more distant from the remaining five species. Species 9 (*A. leonardii*) occupies an intermediate position between this interrelated group and the much less closely linked species 11, 12, 13, and 8 (*A. campanensis*, *A. hartwegiana*, *A. darienensis*, and *A. lingua-bovis*). The tentative position of species 8 merits further discussion. Whereas multidimensional scaling placed species 9 between species 1–7 and 8 based on all crossing relationships, the first connection of species 8 is with species 3 at CI = 0.45. No further connections are made until CI = 0.12 with species 9 (Fig. 55). It is possible that the crossability index between species 8 and 3 is the result of a sampling error due to the unusually small number of crosses attempted ($n = 10$). An initial connection of species 8 (*A. lingua-bovis*) with 9 (*A. leonardii*) would be more in accord with the pattern of crossabilities between species 8 and all other taxa.

NATURAL HYBRIDIZATION AND ISOLATING MECHANISMS

Only two combinations of parental species are suspected of producing naturally occurring hybrid offspring. Three Panamanian localities host putative hybrids between *A. sinclairiana* and *A. gracilis*. All three are mid-elevation sites where cloud forest habitat of *A. gracilis* has been disturbed and warmer and drier local climates result. *Aphelandra sinclairiana* usually occurs along

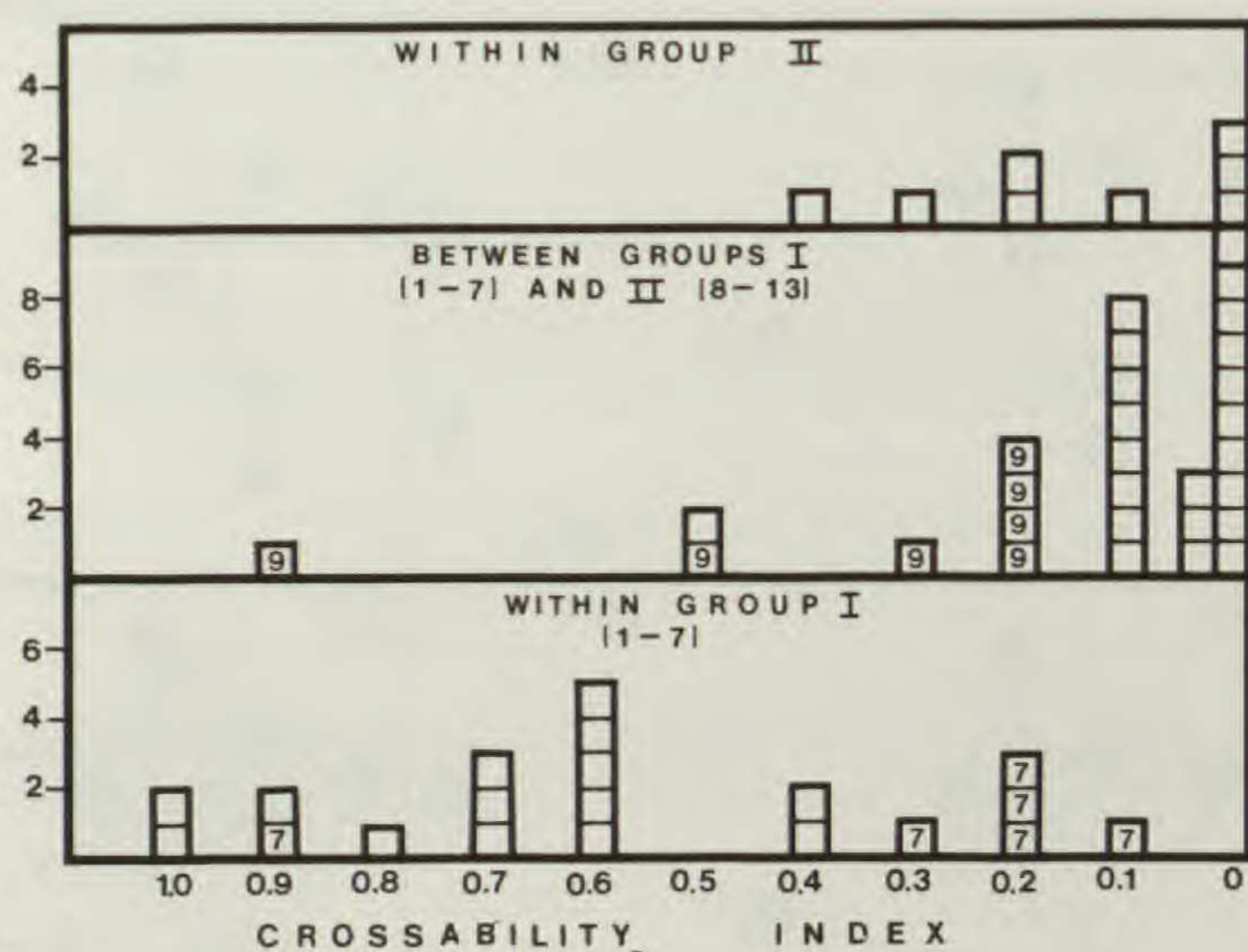
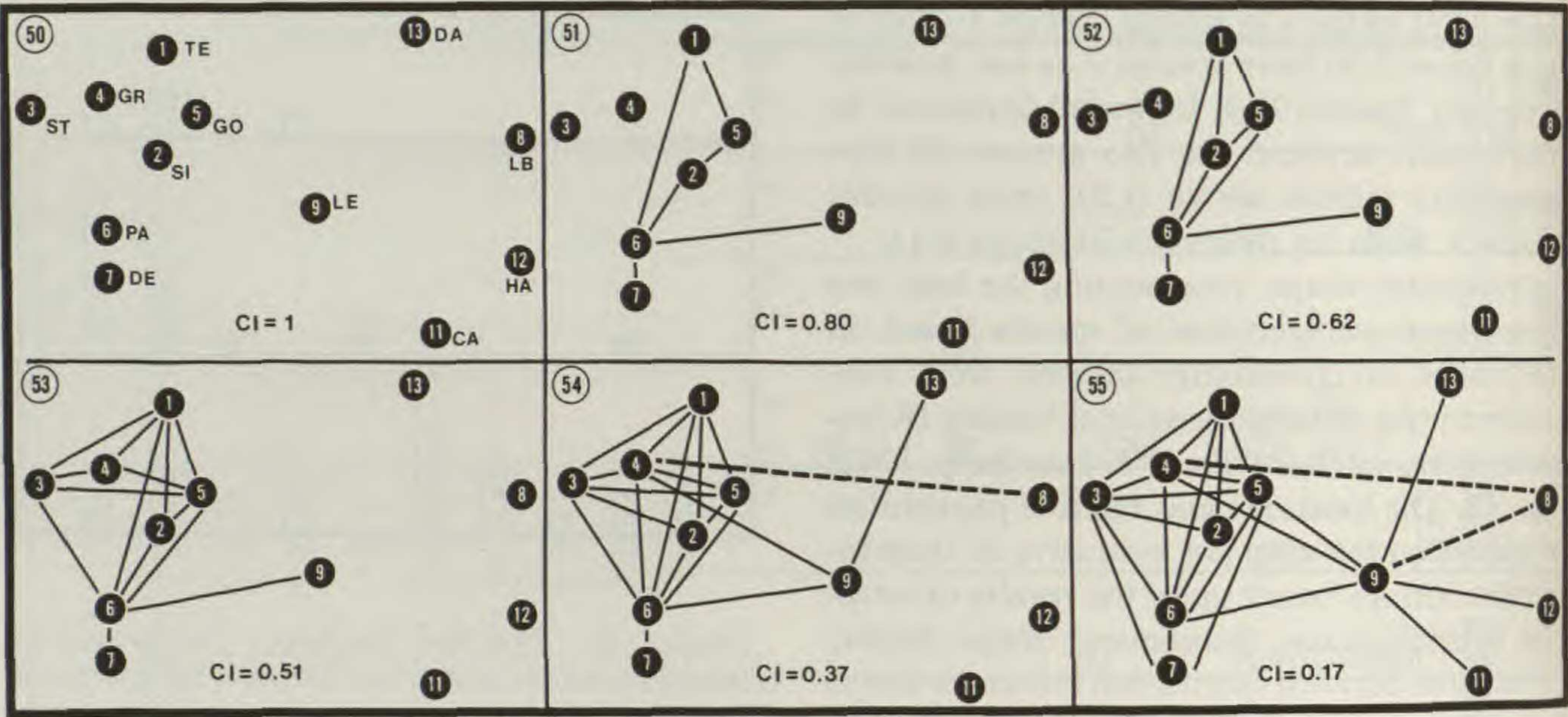


FIGURE 49. Summary frequency distribution of crossability indices within and between the species of Groups I and II. Numbered boxes illustrate points made in text.

edges and in gaps in primary lowland to pre-montane forest, and may also colonize extensively disturbed areas at higher elevations. Hybrid plants between these two species are found in disturbed areas near El Valle (Coclé), Cerro Jefe and El Llano (Panamá) (Fig. 56). They are distinctly intermediate in many characters and produce distorted, apparently sterile pollen. Unfortunately, I have not attempted this cross in the greenhouse.

Interspecific hybrids apparently between *A. sinclairiana* and *A. golfodulcensis* occur at various localities in the Caribbean lowlands of northeastern Costa Rica (Fig. 56). Although the ranges of the two parental species are separated by the central mountain range in Costa Rica, older collections indicate that the two may have occurred close together along either slope of the central plateau north of the high Talamanca range. These localities are mostly urban population centers at the present time. The putative hybrids are intermediate between the two parental species in many features and, though quite vigorous, are pollen sterile. Numerous self- and cross-pollinations between clumps of these plants were attempted without any successful seed set. Collection localities suggest that streams and rivers are important in the propagation of this sterile hybrid. Three clumps of the hybrid occur at La Selva in Heredia province, all of which are along the banks of the Río Puerto Viejo within the flood zone. Branches broken off upstream would root quite readily when lodged against the bank downstream, giving rise to new "individuals" of



FIGURES 50–55. Crossability mapping of Central American species of the *Aphelandra pulcherrima* complex, at six successive levels of crossability. All connections made at and above the indicated CI are presented in each map. Dashed lines indicate conflicting evidence for the position of species 8 as discussed in text.

the hybrid. Hybrids between *A. sinclairiana* and *A. golfodulcensis* have been made in the greenhouse, and these are indistinguishable from the putative hybrids from Costa Rica. Field studies and greenhouse hybridizations indicate that, if the ranges of the two parental species overlapped, compatibility of flowering times, identical pollinator species, and interfertility would result in the production of hybrids.

With these exceptions, reproductive isolation between Central American species of the *A. pulcherrima* complex is apparently complete. For species pairs that are fully allopatric and/or completely intersterile (Table 12), further discussion of isolating mechanisms is moot. The results of greenhouse crosses using plants from field populations, however, indicate that many species with adjacent or sympatric ranges are interfertile. Be-

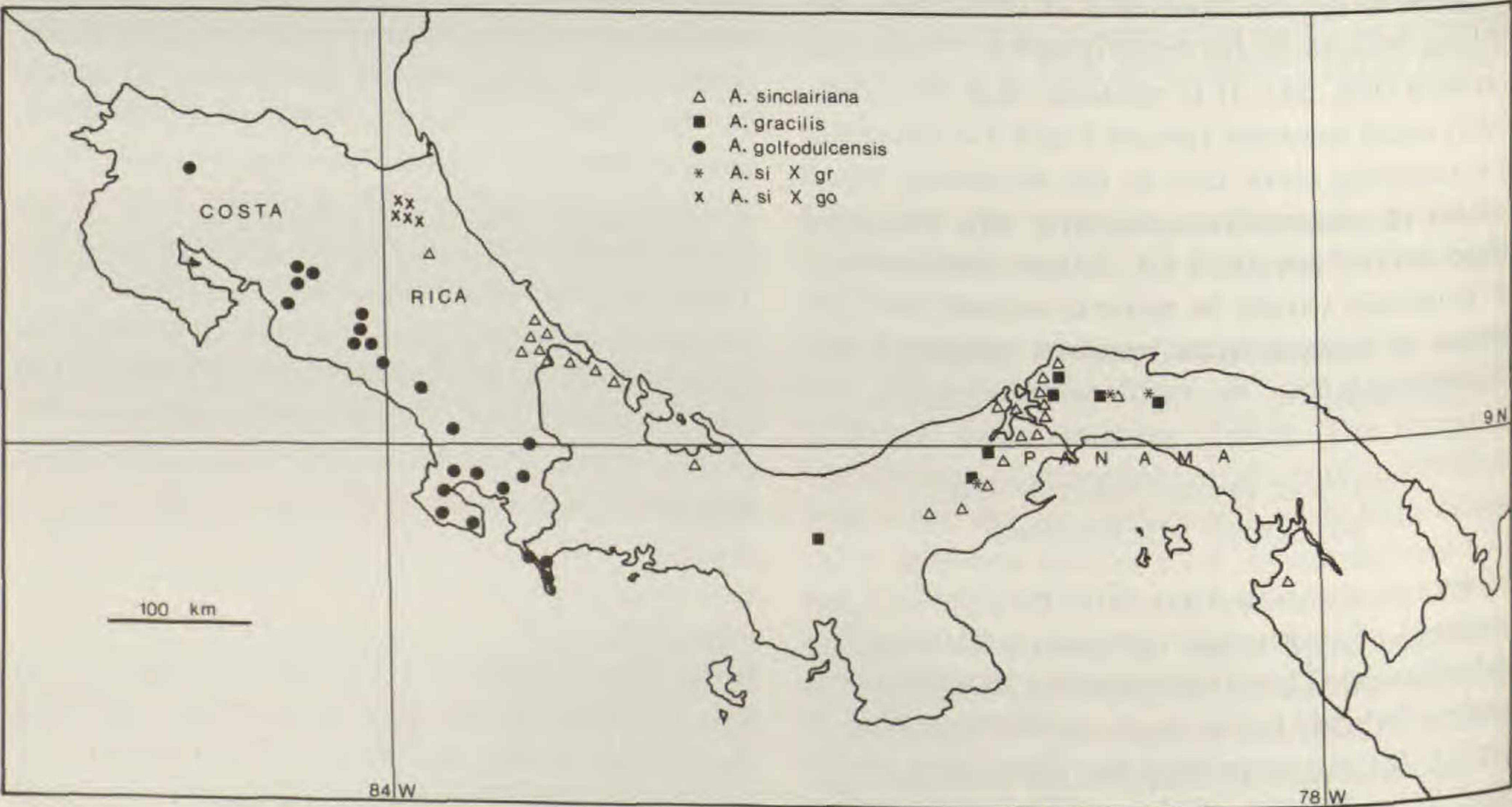


FIGURE 56. Distribution of *Aphelandra sinclairiana*, *A. gracilis*, *A. golfodulcensis*, and the hybrids between each of the latter two species, and *A. sinclairiana* in Costa Rica and Panama.

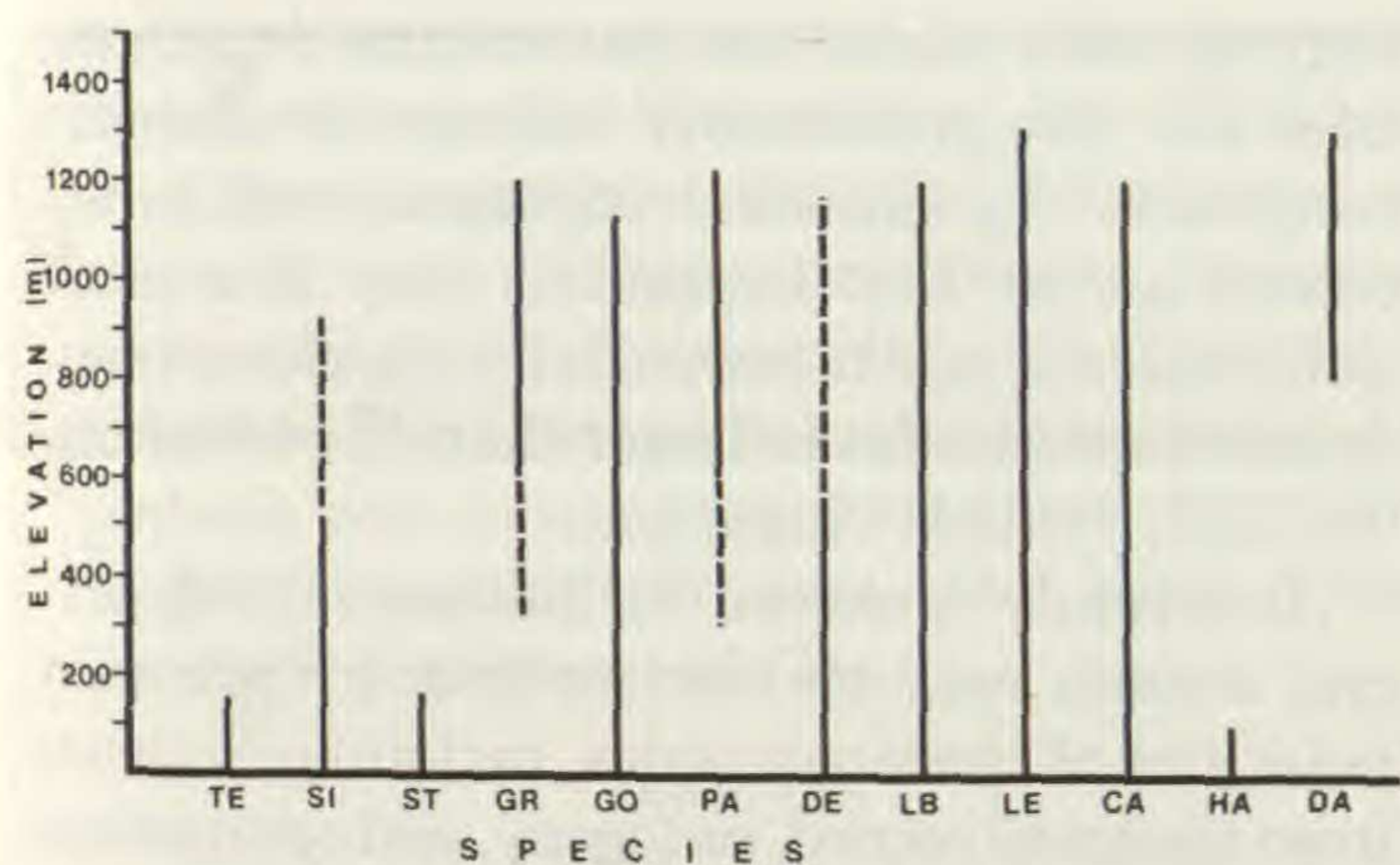


FIGURE 57. Elevational range of the Central American species of the *Aphelandra pulcherrima* complex. Dashed bars indicate elevations at which species are found only when local climatic conditions result in habitat atypical of that elevation in this region.

cause hybrids are rare in nature, further examination of barriers preventing hybridizations between such species is appropriate. Four interrelated factors merit attention: isolation by elevational range, habitat differences, flowering seasonality, and pollinator specificity.

Isolation by elevation, especially if reinforced by similarly restricted pollinator ranges and habitats, may effectively prevent hybridization between species. Several species of *Aphelandra* are restricted to either lowland or mid-elevation localities (Fig. 57). Thus, although the ranges of several lowland species (e.g., *A. deppeana*, *A. sinclairiana*, *A. terryae*) are adjacent to those of mid-elevation species (e.g., *A. panamensis*, *A. gracilis*) (Fig. 56), hybridization events are rare.

Habitat differences may separate species that

have adjacent ranges, or can reinforce elevational isolation. The species of *Aphelandra* treated here are found in seasonally drought deciduous lowland forest, lowland wet forest, and cloud forest. *Aphelandra deppeana*, for example, occurs in habitats with a more severe dry season than can be tolerated by other species. This habitat difference, along with pollinator specificities, apparently reduces the possibility of hybridization involving *A. deppeana*. Thus, although hybrids of *A. deppeana* and its close relative, the cloud forest species *A. panamensis*, are easily synthesized (Table 11), naturally occurring hybrids are not found.

Because the wet and dry seasons are quite discrete in many parts of Central America, temporal differences in flowering can be effective as a barrier to hybridization even between fully sympatric species. Four species of *Aphelandra* treated here flower during the dry season, and the remaining nine flower during the wet season (Table 8). For example, *A. panamensis* and *A. gracilis* coexist and share the same pollinators at several localities in Panama. Lack of overlapping flowering seasons effectively prohibits hybridization.

As documented by field observations of flower visitors to the species of *Aphelandra* treated here, all but *A. deppeana* are pollinated by large hermit or hermit-like hummingbirds (Table 9). Pollinator differences thus reinforce reproductive isolation of *A. deppeana* and species with adjacent ranges (e.g., *A. sinclairiana*). The two main pollinators of the remaining species occupy different elevational ranges, perhaps reinforcing eleva-

TABLE 12. Isolating mechanisms operative between Central American species of the *Aphelandra pulcherrima* complex. Pairs not fully allopatric (A) and/or intersterile (I) may be isolated by elevation (E), habitat (H), flowering seasonality (FS), or pollinator specificity (P). Species numbers and abbreviations as in Table 2.

Species	1. TE	2. SI	3. ST	4. GR	5. GO	6. PA	7. DE	8. LB	9. LE	11. CA	12. HA
2. SI	A										
3. ST	A										
4. GR	A	E,H ^a	A								
5. GO	A	A	A	A							
6. PA	E,FS	E,H,FS	A	FS	A						
7. DE	H,FS,P	H,FS,P	A	E,H,FS,P	H,FS,P	E,H,P					
8. LB	E,FS	H,FS	A,I	A	FS	I	A				
9. LE	A	A	A	E,FS	A	E	A	E			
11. CA	A ^a	E,H,FS ^a	A,I	I	A,I	I	A	A,I	A		
12. HA	FS ^a	A ^a	A	A ^a	A,I	I	A,I	I	E	A	
13. DA	A	A	A	A ^a	A	I	A,I	I	E	A ^a	E,H ^a

^a Species pairs for which data from artificial hybridizations are not available.

tional isolation of geographically proximate species. Long-tailed (lowlands) and green hermits (mid-elevations) are, however, apparently equally effective pollinators of these species. *Aphelandra sinclairiana*, which is usually a lowland species pollinated by long-tailed hermits, is cultivated at 1,200 m at the Las Cruces Botanical Garden in Costa Rica. Visits to flowers by green hermits were apparently effective since these plants set numerous seeds. Similarly, in those parts of its range where disturbance has resulted in the spread of *A. sinclairiana* to mid-elevations, pollinator specificities are lost. Hybridization between *A. sinclairiana* and *A. gracilis*, a species restricted to mid-elevations, results because green hermits pollinate flowers of both species.

The paucity of naturally occurring hybrids is at first striking given the geographic proximity and lack of full sterility between many of these species. However, in the topographically complex terrain of Central America, high mountain ranges and prevailing weather patterns result in small scale environmental partitioning. Under these conditions, isolating factors that fall short of complete intersterility and strict allopatry can effectively prohibit hybridization. Such factors are clearly important among the species of *Aphelandra* treated here.

PHYLOGENETIC ANALYSIS

INTRODUCTION AND METHODS

The goal of phylogenetic systematics (sensu Hennig, 1966) is to classify organisms according to their genealogical relationships. Because a common genealogy is shared by all organisms, phylogeny provides the conceptually unifying basis for biological classification. Provided that only strictly monophyletic taxa are recognized, hierarchical Linnaean classification allows exact retrieval of phylogenetic relationships. Monophyletic groups can be delimited only by recognition of shared derived (advanced) character states (Hennig, 1966; Lundberg, 1972; Wiley, 1981). Character analysis is thus basic to phylogeny reconstruction and involves at least two steps: recognition of strictly homologous characters and formulation of polarity hypotheses. The phylogeny supported by the largest suite of congruent derived character states is the best hypothesis. Homoplasies of several sorts may occur and indicate reversals, parallelisms, and errors in character analysis. Such unreliable characters

may be more numerous than reliable ones in the data set, but presumably will not be mutually congruent. An incorrect phylogeny will be accepted as the best hypothesis only if a set of unrecognized and hierarchically correlated homoplasies exists that is larger than the set of cladistically reliable characters.

As recently reviewed by Stevens (1980), several criteria may be used to infer evolutionary polarities of character states, including evidence from the fossil record, ontogeny, and comparison with out-groups. In this study, primary emphasis was on the last criterion because *Aphelandra* has no known fossil record and the ontogeny of most characters used in the analysis has not been studied. Based upon shared possession of a suite of derived character states that result in the distinctive corolla morphology peculiar to this group, the species of the *A. pulcherrima* complex are hypothesized to be monophyletic. These species, along with *A. hylaea* Leonard, *A. impressa* Lindau, and *A. lamprantha* Leonard, are also unique within *Aphelandra* in having nectaries on the floral bracts. Shared possession of the extra-floral nectaries is evidence that these three species and the *A. pulcherrima* complex are together a monophyletic group, and that one or more of the three is the sister group of the *A. pulcherrima* group. Further resolution of the sister group will require further study; all three species were therefore used as the out-group in character comparisons and polarity decisions. Following study of the distribution of states of 42 characters (Table 13) among these species, polarity hypotheses were made following the out-group method (Watrous & Wheeler, 1981). Consideration of the three species out-group resulted in unambiguous hypotheses for 35 of the 43 characters (2–10, 12–29, 33, 34, 36, 39–43). Character states in the out-group were unknown or offered conflicting evidence for determining evolutionary polarities of the remaining eight characters and the analysis was expanded to consider more distantly related groups. Relationships within the genus are not sufficiently resolved to permit identification of the sister group of the species sharing bracteal nectaries and the entire genus was thus used as the next level of comparison. Two additional, more distantly related out-groups are provided by the relationships of *Aphelandra* within Acanthoideae: other genera in Aphelandreae and the Old World Acantheae. The results of character analysis are presented in Table 13 and as a character by taxon matrix in Appendix E. The value of the phylo-

genetic hypothesis presented for the species of *Aphelandra* treated here rests on the validity of this character analysis. Detailed information on character state distributions among out-group taxa and polarity decisions for each character is available from the author. A phylogenetic hypothesis was constructed from these data using the Wagner method (Wagner, 1969; Kluge & Farris, 1969; Lundberg, 1972).

RESULTS

The 13 species fall into two lineages (Fig. 58) herein referred to as Group I (species 1–7) and Group II (8–13) (Table 3). The species of Group I share several uniquely derived character states: trichomes of distal stems longer than 0.5 mm (character 4); bracteal nectaries of individual, large glands (12, 13); terete fruits (30); sub-globose seeds (35); and semi-hypogeal germination (37) (Fig. 58). Shared possession of these advanced states provides strong evidence of a monophyletic origin of these species. *Aphelandra sinclairiana* (species 2) and *A. storkii* (3) are sister species, sharing long and erect trichomes on distal stems (character 3). *Aphelandra terryae* (1) is hypothesized to be the sister group of these two species. Characters providing evidence for this relationship are, however, homoplasious (reversed or paralleled elsewhere in the cladogram) (Appendix F). *Aphelandra deppeana* (7) and *A. panamensis* (6) are sister species, sharing three uniquely derived character states: dense pubescence of distal stems (2), villous pubescence of lower corolla lip (26), and oblique stigmas (29). The relationships of *A. golfodulcensis* (5) and *A. gracilis* (4) within Group I are tentative. Shared possession of green floral bracts (9), along with six homoplasious characters (Appendix F), suggests that these two species share a monophyletic origin with *A. deppeana* and *A. panamensis*. In conflict with this evidence, *A. deppeana* and *A. panamensis* share derived states of characters 25 (pubescence of the corolla tube) and 26 (long trichomes on the lower lip of the corolla) with *A. terryae* (1), *A. sinclairiana* (2), and *A. storkii* (3).

Evidence in support of a monophyletic origin of species 8–13 (Group II) is provided by shared possession of extremely leathery floral bracts (character 7) and glabrous corollas (25, 26) (Fig. 58). The bracteal nectaries composed of many, minute glands facilitates recognition of these species. This feature, however, is shared by the three species out-group (*A. hylaea*, *A. impressa*,

A. lamprantha) and is thus hypothesized to be primitive for the *A. pulcherrima* complex. The placement of *A. lingua-bovis* (species 8) is tentative. All of the derived character states it possesses are homoplasious (Appendix F). Derived states of characters 23 (narrow upper corolla lip), 28 (anther length) and 39 (syntrophic pollen) suggest a relationship between this species and the sister species *A. deppeana* (7) and *A. panamensis* (6). This relationship, however, is contradicted by many other characters. Study of South American relatives of *A. lingua-bovis* may provide data for a more satisfactory resolution of the phylogenetic relationships of this species. Strong evidence for a monophyletic origin of species 9–13 (*A. leonardii*–*A. darienensis*) is provided by shared uniquely derived states of characters 40 (pollen with unsculptured longitudinal bands) and 41 (corolla opening immediate). *Aphelandra laxa* (10) shares leathery and papillate corollas (21, 41) with species 11–13. Shared possession of falcate bracteoles (16) and large seeds (36) provides evidence that *A. campanensis* (11), *A. hartwegiana* (12), and *A. darienensis* (13) are monophyletic. *Aphelandra hartwegiana* and *A. darienensis* share anthers longer than 9 mm (28), as well as three homoplasious derived character states (Appendix F). In conflict with this evidence are characters 19 (calyx lobes obtuse and apiculate) and 5 (parallel evolution of pedunculate inflorescences), which suggest that *A. hartwegiana* and *A. campanensis* are sister species. Additional data will be required to satisfactorily resolve these relationships.

The *A. pulcherrima* complex includes about 25 species that occur only in South America (Appendix A). These species received only cursory attention in the course of this research and have not been incorporated into the phylogeny. It is apparent that the species treated here do not comprise a single, monophyletic sister group of all South American species. Rather, each of the Central American groups described here has South American members. The Central American species thus represent more than one evolutionary line from the older continent. As detailed in the taxonomic treatment, several species apparently have closer relatives among South American members of the complex than among species treated here. Further study of South American species of this complex will permit expansion of the phylogeny to include all species of the monophyletic group. The complete cladogram will facilitate formulation of biogeographic

TABLE 13. Characters and character states used in phylogenetic analysis. Asterisks denote hypothesized primitive states. For multistate characters with an intermediate state primitive, two-directional evolution is hypothesized.

-
1. Habit
 - *0 Monocaulous
 - 1 Shrub/small tree
 2. Pubescence of distal stem, density
 - *0 Sparse
 - 1 Moderate
 - 2 Dense
 3. Pubescence of distal stem, orientation
 - 0 Erect
 - *1 Upwardly appressed
 - 2 Downwardly appressed
 4. Pubescence of distal stem, length
 - *0 to 0.5 mm
 - 1 0.6–1 mm
 - 2 >1 mm
 5. Inflorescence
 - *0 Sessile
 - 1 Pedunculate
 6. Floral bracts, margin
 - *0 Toothed
 - 1 Occasional minute teeth
 - 2 Entire
 7. Floral bracts, texture
 - *0 Membranous
 - 1 Coriaceous
 - 2 Leathery
 8. Floral bracts
 - *0 Imbricate
 - 1 Lax
 9. Floral bracts, color
 - *0 Green
 - 1 Brightly colored
 10. Floral bracts, length
 - 0 <8 mm
 - *1 8.5–14 mm
 - 2 14.5–22 mm
 - 3 22.5–30 mm
 - 4 >30 mm
 11. Floral bracts, apex
 - *0 Acute
 - 1 Obtuse
 12. Bracteal nectaries
 - *0 Many minute
 - 1 Few large
 13. Bracteal nectaries, diameter
 - *0 <0.25 mm
 - 1 0.25–0.75 mm
 - 2 0.76–1 mm
 - 3 >1 mm
-

TABLE 13. Continued.

-
14. Bracteal nectaries, position
 - 0 Sub-medial
 - *1 Medial
 - 2 Supra-medial
 15. Floral bracts, orientation
 - *0 Plane
 - 1 Recurved
 16. Bracteoles, shape
 - *0 Lance-ovate
 - 1 Slightly falcate
 - 2 Falcate
 17. Bracteoles, color
 - *0 Green
 - 1 Brightly colored
 18. Calyx, length
 - *0 6–10 mm
 - 1 11–15 mm
 - 2 16–20 mm
 19. Sepals, apical shape
 - *0 Acute
 - 1 Obtuse and apiculate
 20. Sepals, color
 - *0 Green
 - 1 Brightly colored
 21. Corolla, texture
 - *0 Membranous
 - 1 Coriaceous
 - 2 Leathery
 22. Corolla, length
 - 0 <5 cm
 - *1 5.1–6 cm
 - 2 6.1–7 cm
 - 3 >7 cm
 23. Corolla, width upper lip
 - 0 ≤6 mm
 - 1 6.5–9 mm
 - 2 9.5–11.5 mm
 - 3 ≥12 mm
 24. Corolla, apical shape upper lip lobes
 - *0 Acute to acuminate
 - 1 Emarginate and apiculate
 25. Corolla tube, pubescence
 - 0 Glabrous
 - *1 <0.25 mm
 - 2 >0.25 mm
 26. Corolla, pubescence of lower lip
 - 0 Glabrous
 - *1 <0.25 mm
 - 2 0.26–0.75 mm
 - 3 >0.75 mm
 27. Corolla, color
 - *0 Red, pink, orange
 - 1 Yellow
-

TABLE 13. Continued.

28. Anther, length	
0 1–3 mm	
*1 3.5–6 mm	
2 6.5–9 mm	
3 >9 mm	
29. Stigma, morphology	
*0 Bilobed	
1 Oblique	
30. Fruit, shape	
*0 Flattened	
1 Terete	
31. Fruit, color (immature)	
*0 Other	
1 Orange-brown	
32. Fruit, color (immature)	
*0 Other	
1 Black	
33. Fruit, length	
*0 <20 mm	
1 21–25 mm	
2 26–30 mm	
3 >30 mm	
34. Fruit, vestiture	
*0 Glabrous	
1 Puberulous	
35. Seed, shape	
*0 Flattened	
1 Sub-globose	
36. Seed, diameter	
0 <4 mm	
*1 4.5–6 mm	
2 >6.5 mm	
37. Germination pattern	
*0 Epigeal	
1 Semi-hypogeal	
38. Pollen, shape (L/W)	
*0 L/W < 2.1	
1 L/W > 2.1	
39. Pollen, colpi	
*0 Tricolpate	
1 Synticolpate	
40. Pollen, sculpturing	
*0 Continuous	
1 Unsculptured bands	
41. Corolla opening	
*0 Delayed	
1 Immediate	
42. Corolla, vestiture	
*0 Pubescent, glabrous	
1 Papillate	
43. Fruit, shape	
*0 Stipitate	
1 Sessile	

hypotheses based on phylogenetic relationships and distributional patterns.

COMPARISON OF RESULTS FROM ARTIFICIAL HYBRIDIZATIONS AND PHYLOGENETIC ANALYSIS

The results of artificial hybridizations can be compared with two measures of relationship derived from phylogenetic analysis: number of hypothesized speciation events (cladistic distance) and number of inferred evolutionary changes (patristic distance) between species. Both distances are significantly correlated with crossability indices for each pair of species ($r = 0.442$, cladistic distance; $r = 0.560$, patristic distance; 57 df, $P < 0.001$ for both coefficients). More specific comparisons of the results of the two analyses are made using Figures 55 and 58. Phylogenetic analysis separates the species into two lineages (Fig. 58). Crossability indices generally support this division but suggest an intermediate position for *A. leonardii* (species 9) between the two groups (Fig. 55). Both analyses closely link *A. terryae*, *A. sinclairiana*, *A. storkii*, *A. golfo-dulcensis*, *A. gracilis*, and *A. panamensis* (species 1–6). The phylogenetic hypothesis that *A. deppeana* and *A. panamensis* are sister species is supported by high crossability between the two (Table 11). *Aphelandra deppeana* has several uniquely derived character states that distinguish it from other species of Group I (Fig. 58). Low crossability of *A. deppeana* with other species of Group I corroborates its distinctiveness (Table 11, Fig. 55).

The most apparent difference in the results of the two analyses is in respect to interrelationships of Group II (species 8–13). Phylogenetic analysis suggests that species of Group II are as closely interrelated as those of Group I. The available results of artificial hybridizations, however, indicate that these species do not cross readily (Table 11, Fig. 55). This conflict illustrates the difficulty encountered in using artificial crossability to estimate relationships. The rigidity of genetic incompatibility barriers to hybridization between species is apparently not reliably correlated with phylogenetic relationships. The efficacy of other isolating mechanisms may be important: distant relatives separated by effective barriers (e.g., habitat, different pollinators) may remain cross-compatible while sister species lacking additional isolating mechanisms may be highly intersterile. Thus, if genetic incompatibility is relatively unimportant as a barrier to interbreeding

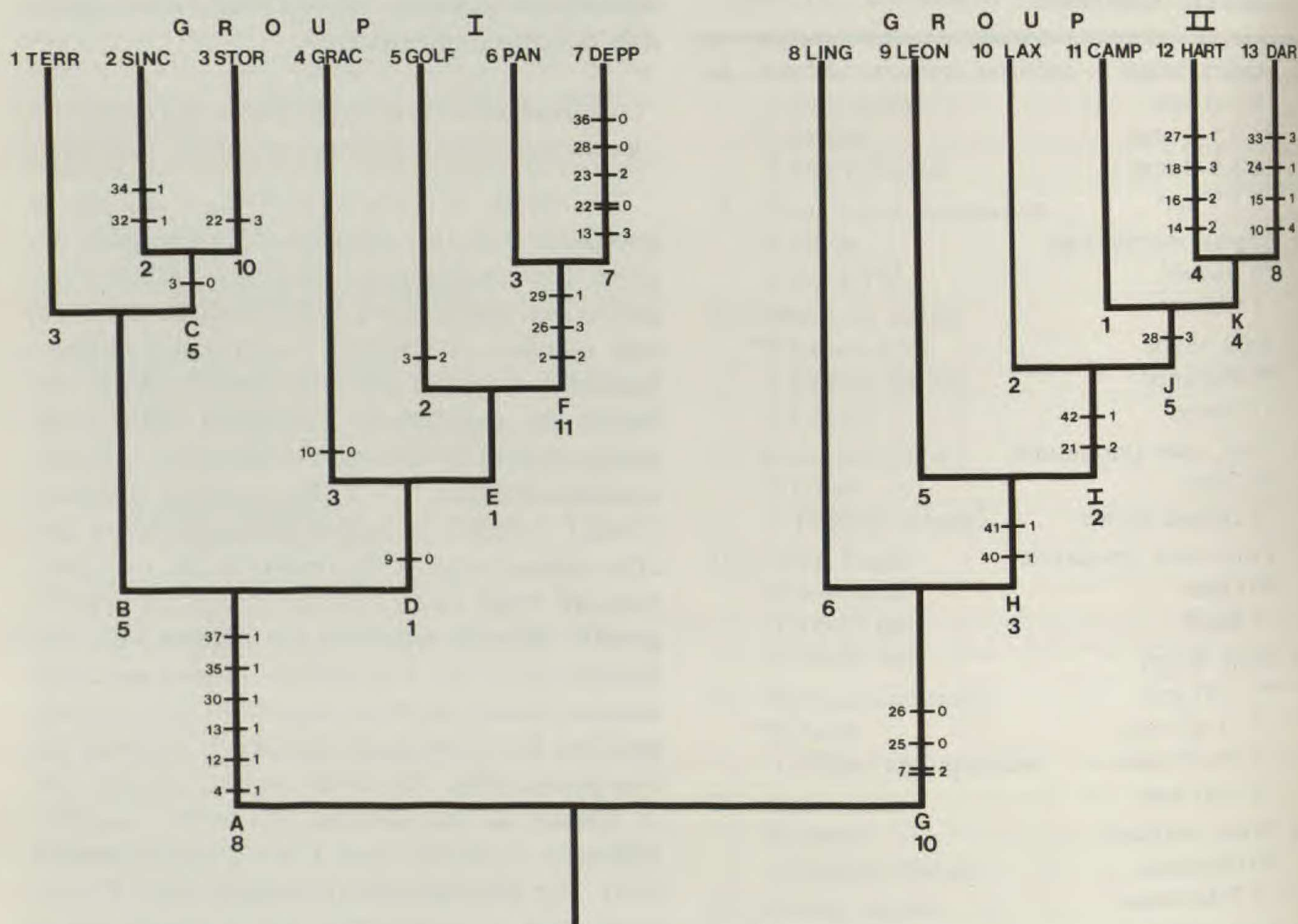


FIGURE 58. Phylogenetic hypothesis of relationships among the Central American species of the *Aphelandra pulcherrima* complex. Each species is located along the upper horizontal of the diagram. Evolution of uniquely derived and unreversed character states is indicated by horizontal slashes, with numerals to the left indicating the changing character and those to the right indicating the state evolved. Non-terminal intervals are identified by letter. Total length (including homoplasies) is given for each interval. Appendix F provides a complete listing of character changes by interval.

among species of Group I, then the results of artificial hybridizations may provide reliable estimates of degree of phylogenetic relationships among these species. In Group II, genetic incompatibility may be more important, resulting in strong intersterility barriers between species.

TAXONOMIC TREATMENT

Aphelandra R. Br., Prodr. 475. 1810. LECTOTYPE: *A. cristata* Jacq.

Synandra Schrader, Gött. Gel. Anz. 1: 715. 1821, non Nuttall 1818.

Amathea Raf., Fl. tellur. 10: 65. 1838.

Strobilorrhachis Klotzsch in Otto & Dietrich, Allg. Gartenzeitung 7: 307. 1839.

Hydromestus Scheidw. in Otto & Dietr., Allg. Gartenzeitung 10: 285. 1842.

Hemisandra Scheidw., Bull. Acad. Roy. Sci. Bruxelles 9: 22. 1842.

Lagochilium Nees in Martius, Fl. bras. 9: 85. pl. 10. 1847.

Perennial suffrutescent herbs to diffusely branched shrubs, rarely sub-rosettes or small trees; stems terete to quadrangular, soft-wooded, rarely thick and succulent, glabrous to pubescent, nodes frequently swollen. Leaves opposite, rarely verticillate or alternate, petiolate; the blades membranous to coriaceous, marginally toothed, lobed, crenate, undulate or entire; stipules lacking or present as interpetiolar spines. Inflorescences of terminal spikes, solitary to few, or numerous and arranged in a freely branching paniculate inflorescence; each flower subtended by a bract, these small, green and loosely arranged, to large, imbricate, and highly colored, marginally toothed or entire, occasionally bearing lateral glandular areas ("ocelli"); bracteoles two, laterally subtending calyx, usually lanceolate, similar to sepals in shape and texture, rarely rudimentary. Calyx of 5 subequal, usually lanceolate sepals, the adaxial sepal, and the abaxial

and lateral pairs of unequal width; corolla straight or curved, limb 5-parted, nearly regular to strongly bilabiate with a basically bilobed upper lip (the lobes sometimes partially or completely united) and a reflexed 3-lobed lower lip, the lobes of the lower lip subequal to strongly dimorphic with lateral lobes reduced or essentially lacking; stamens four, epipetalous, rarely included within corolla tube, usually exerted beyond throat but not extending beyond tip of upper lip, anthers usually borne erectly, within or closely parallel-

ing upper lip, narrow, one-celled; stigma infundibular, entire or shallowly bilobed, style filiform, frequently extending through and slightly beyond the adaxial pair of anthers, ovary bilocular with two ovules per locule. Fruits capsular, clavate to sub-globose, terete to strongly flattened, 4-seeded, explosively dehiscent on drying, seeds borne on hook-like retinacula, brown, rounded to somewhat angled and strongly flattened to sub-globose. Seed germination epigeal or semi-hypogeal.

KEY TO THE CENTRAL AMERICAN SPECIES OF THE *APHELANDRA PULCHERRIMA* COMPLEX

1. Bracteal nectaries composed of a few (1–10) well-defined glands each 0.5–1.25 mm in diameter; capsules terete in cross-section or nearly so; seeds sub-globose (diameter/width < 2/1).
 2. Corolla less than 4.5 cm long; S Mexico to N South America 7. *A. deppeana*
 - 2'. Corolla exceeding 5 cm long.
 3. Bracts consistently bearing 2–3 pairs of marginal teeth, each 1–2 mm long; capsules sessile; leaves epetiolate; central and eastern Panama 6. *A. panamensis*
 - 3'. Bracts marginally entire or occasionally bearing 1–2 pairs of minute teeth (< 1 mm long); capsules stipitate; leaves with distinct petiole.
 4. Plants profusely branched shrubs to small trees with many short (to 20 cm) spikes in a terminal panicle inflorescence; bracts narrowly to broadly ovate, to 20 mm long.
 5. Bracts green to occasionally dull brown-orange, narrowly ovate to ovate, to 7 mm wide.
 6. Bracts 5–8 mm long, non-imbricate, internodes 7–10 mm long; leaves glabrous, slightly coriaceous and shiny; central Panama 4. *A. gracilis*
 - 6'. Bracts > 8 mm long, slightly to closely imbricate; leaves pubescent, membranous, and dull.
 7. Bracts slightly imbricate, apically obtuse, sparsely pubescent; pubescence of distal stems erect; corolla pubescent; central Panama *A. gracilis* × *sinclairiana*
 - 7'. Bracts imbricate, apically acute, minutely puberulent; pubescence of distal stems downwardly appressed; corolla minutely puberulent; SW Costa Rica and adjacent Panama 5. *A. golfodulcensis*
 - 5'. Bracts bright orange, broadly ovate, 8–20 mm wide.
 8. Corollas 5.7–6.2 cm long; distal stems, leaves and bracts sparsely pubescent; E Panama and Colombia 1. *A. terryae*
 - 8'. Corollas 6.4–7.1 cm long; distal stems, leaves and bracts moderately pubescent to pilose.
 9. Bracts 16–21 mm long, 14–20 mm wide, densely pubescent; distal stems pilose, trichomes erect; anthers 7–8 mm long, fertile; immature capsules dark, pubescent; S Costa Rica to E Panama 2. *A. sinclairiana*
 - 9'. Bracts 9–13.5 mm long, 5–9 mm wide, sparsely pubescent; distal stems moderately pubescent, trichomes downwardly appressed; anthers 6–6.5 mm long, shriveled and producing little pollen; plants sterile; NE Costa Rica *A. golfodulcensis* × *sinclairiana*
 - 4'. Plants sparsely branched or monocaulous sub-shrubs with one or few long (to 45 cm) terminal spikes; bracts rhombic oblong-ovate, ≥ 25 mm long; Costa Rica (Limón and Heredia) 3. *A. storkii*
- 1'. Bracteal nectaries of many (> 50) minute glands forming oblong patches 2–5 mm in diameter; capsules strongly flattened; seeds strongly flattened (diameter/width > 3/1).
 10. Corolla 5.5–6 cm long; plants rarely taller than 1.5 m; immature capsules orange-brown; SW Costa Rica, Panama, and Colombia 8. *A. lingua-bovis*
 - 10'. Corolla longer than 6 cm; plants taller than 1.5 m when reproductive; immature capsules green or yellow-green.
 11. Bracts non-imbricate, separated by internodes 1.5–2 cm long; Panama (San Blas) 10. *A. laxa*
 - 11'. Bracts imbricate, internodes not visible at anthesis.
 12. Bracts rhombic-ovate, 7–10 mm long, 5–7 mm wide; bracteoles lanceolate; Costa Rica and Panama 9. *A. leonardii*
 - 12'. Bracts broadly ovate, 11–40 mm long, 9–26 mm wide; bracteoles slightly to markedly falcate.
 13. Bracts to 14 mm long, planar; sepals longer than bracts; capsules to 31 mm long.
 14. Bracts 9–11 mm wide; bracteoles slightly falcate, 11–13 mm long; sepals 15–

- 18 mm long; corolla orange; capsules 20–24 mm long; S Costa Rica (Limón) to central Panama 11. *A. campanensis*
 14'. Bracts 11–14 mm wide; bracteoles strongly falcate, 7–10 mm long; sepals 17–22 mm long; corolla yellow (rarely orange) and extremely coriaceous; capsules 28–31 mm long; E Panama and Colombia 12. *A. hartwegiana*
 13'. Bracts 30–40 mm long, apically recurved; sepals shorter than bracts, not visible at anthesis; capsules about 35 mm long; Panama (Darién) 13. *A. darienensis*

1. ***Aphelandra terryae*** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 381. 1940. TYPE: Panama. Darién: Chepigana District, Tucutí, ca. sea level, *Terry & Terry 1377* (holotype, F; isotype, GH).

Aphelandra incarnata Leonard, Contr. U.S. Natl. Herb. 31: 242. 1953. TYPE: Colombia. Santander: vicinity of Barranca Bermeja, Magdalena Valley, 100–500 m, *Haught 1315* (holotype, US).

Shrubs 1–4 m high, profusely branching; younger stems subquadrangular, moderately pubescent, the trichomes downwardly appressed, white, about 0.25 mm long, older stems terete, glabrate. Leaves opposite (very rarely alternate), oblanceolate, 20–30 cm long, 6–10 cm wide, apically acuminate (the tip acute or blunt), basally attenuate and decurrent on the petiole, marginally entire to slightly undulate; glabrous above and below except veins moderately to sparsely pubescent, the trichomes appressed, white, about 0.25 mm long; petioles 1–2 cm long, sparsely pubescent, the trichomes appressed, white, about 0.25 mm long; leaves subtending inflorescences much reduced, 7–11 cm long, 2.5–4 cm wide, essentially glabrous. Inflorescences terminal, spikes numerous, terete, 3–8 cm long, 1–2 cm wide, arranged in a freely branching paniculate inflorescence; the peduncles 2.5–4 cm long, moderately pubescent, the trichomes erect, white, about 0.25 mm long; rachis minutely puberulous; lowermost 1–2 pairs of bracts leaf-like, 1–2 cm long, 0.5–1 cm wide; floral bracts imbricate, broadly ovate, apically obtuse, marginally entire, 10–12 mm long, 8–10 mm wide, orange, frequently fading to green at base, glabrous within, moderately pubescent without, the trichomes appressed, white, 0.5–0.75 mm long, margins minutely ciliate, the nectaries medial, composed of several (5–12) individual glands, each 0.5–0.75 mm in diameter; bracteoles narrowly ovate, apically acute, 4.5–6 mm long, 2–2.5 mm wide, orange fading to green toward base, glabrous or with moderately pubescent keel, the trichomes appressed, white, about 0.5 mm long. Sepals 6–7 mm long, apically acute, greenish orange, essentially glabrous, the adaxial segment narrowly

ovate, 3–4 mm wide, the abaxial pair lanceolate, 2–2.5 mm wide, the lateral pair narrowly lanceolate, 1.25–1.5 mm wide; corolla pink or orange, 5.7–6.2 cm long, sparsely pubescent except lower lip moderately pubescent, the trichomes erect, white, 0.5–0.75 mm long, the tube 42–45 mm long, about 3 mm in diameter at base, constricted to about 1.5 mm above ovary (7 mm above base), expanding to 6–7 mm deep at throat, the upper lip erect, ovate, 16–18 mm long, 7.5–11.5 mm wide, bilobed, the lobes triangular, 8–9 mm long, anther pocket well-developed, the middle lobe of lower lip broadly lanceolate, 23–26 mm long, 7–8 mm wide, minutely apiculate at apex, the lateral lobes about 1 mm long and 6–7 mm wide; filaments inserted 11 mm from base of corolla tube, free portion of each about 4 cm long, the anthers 5–6 mm long, extending 4–5 mm from tip of upper lip, pollen pale orange; stigma pink, minutely bilobed, the style filiform, extending 3–5 mm beyond the anthers, the ovary apically red, glabrous. Capsules clavate, terete, glabrous, green with red-tinged apex when immature, becoming dark brown to black at dehiscence, 17–19 mm long, 4.5–6 mm wide, 5–6 mm thick, strongly constricted 4–5 mm above base to form narrow stipe; seeds dark brown, 3–4.5 mm in diameter, 1.5–2 mm thick. Seed germination semi-hypogeal.

Habitat and distribution. This species occurs in eastern Panama in the provinces of Darién and San Blas, and in adjacent Colombia. *Aphelandra terryae* is found primarily in lowland forests (occasionally to 500 m elevation) where seasonality of rainfall is not pronounced [tropical moist and wet forests (Holdridge, 1967)]. Individuals of this species are found in gaps in primary forest and along forest edges (streams, trails).

Flowering and fruiting. Peak flowering is during the driest months of the year (Dec. through March). Fruits mature during the late dry season and early wet season.

Leonard (1953) described *A. incarnata*, based on Colombian plants, as distinct from *A. sinclairiana*, and apparently overlooked the earlier

description of essentially identical Panamanian plants as *A. terryae* by Standley (in Standley & Steyermark, 1940). Although I have been unable to study Colombian plants in the field, herbarium specimens are not distinguishable from collections of *A. terryae*. I therefore concur with Wasshausen's (1975) decision to synonymize *A. incarnata* Leonard under *A. terryae* Standley.

Plants of *A. terryae* are distinguished from close relatives by their overall sparse vestiture, size and color of the bracts, short inflorescences and corollas, and green, glabrous capsules.

Relationships. *Aphelandra terryae* is a member of Group I, which includes species with bracteal nectaries of individual, large glands. Phylogenetic analysis indicates that it is most closely related to *A. sinclairiana* and *A. storkii* (Fig. 58). These three species share bright orange floral bracts, bracteoles and sepals, and long trichomes on the corollas.

Additional specimens examined. PANAMA. DARIÉN: W slopes of Cerro Pirre, *Mori & Kallunki* 5516 (MO); Río Pirre near town of Pirre, *Gentry & Clewell* 6937 (F, MO); Río Pirre near crossing of trail from El Real to Tucutí, 20 mi. W of Tucutí, *Duke* 5187 (MO); trail between Pinogana and Yaviza, *Allen* 256 (A, MO, US); Cerro Piriaque, *Tyson et al.* 3815 (DUKE, FSU, MO); trail from Pucuro to Cerro Mali, ridge between Pucuro and Tapalisa Rivers, *Gentry & Mori* 13550 (MO); near helipad at hydrocamp on Río Mortí, *Duke* 15421 (US). SAN BLAS: mainland opposite Achituppu, *Lewis et al.* 126 (GH, MO, US).

COLOMBIA. ANTIOQUIA: along Río Anorí, Zaragoza, 500 m, *Soejarto & Villa* 2734 (GH); Malena, 140–160 m, *Pennell* 3782 (US); between Río Guapá and León, 100 m, *Yepes et al.* 18300 (US); La Llorona near Dabeiba, highway to Mutatá, *Barkley & Gutierrez* 35442 (US). BOLÍVAR: Boca Verde, on Río Sinú, *Pennell* 4581 (NY). CHOCÓ: near Ciudad Mutis, Bahía Solano, sea level–75 m, *Killip & Garcia* 33576 (US); hydrocamp 15, on Río Curiche, 100 m, *Duke* 15380 (US). CUNDINAMARCA: San Antonio, 200 m, *Haught* 6243 (NY, US). SANTANDER: Magdalena Valley between Sogamoso and Colorado Rivers, 100–500 m, *Haught* 2098 (F, NY, US).

2. *Aphelandra sinclairiana* Nees in Benth., Bot. Voy. Sulphur 146. pl. 47. 1844. TYPE: Panama. Province not given, *Sinclair s.n.* (holotype, K, not seen).

Shrubs 2–6 m high, profusely branched; stems terete, younger surfaces moderately pilose, trichomes erect, white, 1–1.5 mm long, older surfaces sparsely pilose to glabrate. Leaves opposite, elliptic to oblanceolate, 20–30(–40) cm long, 6–10(–15) cm wide, apically acuminate to atten-

uate, basally attenuate and decurrent on petiole, marginally entire to slightly undulate, upper surface sparsely strigose, the trichomes appressed, white, about 1 mm long, sparingly pilose below (moderate on veins), the trichomes appressed (erect on veins), white, about 1 mm long; petioles 1–2 cm long, sparingly pilose, the trichomes erect, white, 1–1.25 mm long. Inflorescences terminal, spikes numerous, terete, 8–15(–20) cm long, 2 cm wide, arranged in a freely branching paniculate inflorescence; peduncles lacking or to 6 cm long, moderately pilose, the trichomes erect, white, 1–1.25 mm long; rachis densely pubescent, the trichomes erect, white, about 0.5 mm long; lowermost 2–3 pairs of bracts sterile and leaf-like; floral bracts densely imbricate, broadly obovate, apically obtuse, marginally entire or with 2–3 pairs of minute teeth, 16–20 mm long, 14–20 mm wide, orange, densely minutely puberulous within, densely pubescent without, the trichomes appressed, white, about 0.25 mm long, margins ciliate, the trichomes white, 0.5–0.75 mm long, the nectaries medial, composed of several (4–10) individual glands, each about 0.5 mm in diameter; bracteoles narrowly ovate, apically acute, 7–9 mm long, 2–3 mm wide, orange, moderately pubescent, the trichomes appressed, white, about 0.25 mm long. Sepals 7–9 mm long, apically acute, orange, striate, very minutely puberulous, the adaxial segment oblong, 2–3 mm wide, the abaxial pair lanceolate, 2 mm wide, the lateral pair lanceolate, 1.5 mm wide; corolla pink or orange-red (rarely white), 6.5–7 cm long, moderately pubescent, the trichomes erect, white, 0.5–0.75 mm long, the tube 48–50 mm long, 3 mm in diameter at base, constricted slightly to 1.5–2.5 mm above ovary (8–11 mm above base), expanding to 8–10 mm deep at throat, the upper lip ovate, 16–20 mm long, 9–10 mm wide, bilobed, the lobes triangular, 7–9 mm long, anther pocket well-developed, the middle lobe of lower lip elliptic, 25–29 mm long, 8–10 mm wide, recurled slightly at tip, the lateral lobes 1–2 mm long, 8–9 mm wide; filaments inserted about 11 mm above base of corolla tube, free portion of each about 5 cm long, the anthers 7–8 mm long, extending to within 2–6 mm from tip of upper lip, pollen orange; stigma pink, minutely bilobed, the style filiform, extending 2–5 mm beyond anthers, the ovary glabrous. Capsules clavate, terete, dark brown to black when immature and at dehiscence, very minutely puberulous, 23–25 mm long, 6–7 mm wide, 5–6 mm thick; seeds dark brown, orbicular, slightly flattened, 5–6 mm in

diameter, 2–3 mm wide. Seed germination semi-hypogeal.

Habitat and distribution. *Aphelandra sinclairiana* ranges from southern Costa Rica to eastern Panama (Fig. 56). In Costa Rica, numerous collections of this species have come from the wet Caribbean lowlands of southern Limón province. A collection from Atirro, Cartago by Donnell Smith in 1896 is apparently *A. sinclairiana*, but lack of collections between this locality and southern Limón make it difficult to determine the northern limit of this species. This is true as well of the eastern distributional limit: in addition to numerous collections from central Panama (east to Cerro Brewster), one specimen from the Pacific coast of the Darién is apparently of this species. Additional collections from intervening areas, particularly the Caribbean lowlands of San Blas and Bocas del Toro will help to resolve the distributional limits of this species.

Aphelandra sinclairiana is primarily a species of the seasonally dry lowlands [Holdridge's (1967) tropical moist forest]. Although it is not found in areas with severe dry seasons of long duration, it does occur in seasonally partially deciduous forests that experience a 2–4 month period with markedly reduced precipitation. *Aphelandra sinclairiana* occurs in small to large gaps in primary forest, but also colonizes disturbed edge habitats. Although primarily a lowland species, it occurs occasionally at mid-elevations (to 1,200 m), especially where disturbed cloud forests [premontane wet forests (Holdridge, 1967)] are located at the crest of the central mountain range adjacent to extensive lowland, seasonally dry areas.

Flowering and fruiting. Individuals flower during the driest months of the year (Dec. through March) with apparently very little variation. Most plants have completed fruiting by the onset of the wet season.

Aphelandra sinclairiana may be readily distinguished from other species by its pilose stems, leaves and corollas; large, bright orange bracts; citrus-like odor of the inflorescences and distinctively colored, puberulous capsules. There is some variability in bract size and, most notably, corolla color in this species. I have found plants with pink, red-orange, and white corollas at the same locality. These differences are apparently not of systematic importance.

Relationships. Phylogenetic analysis indicates that *A. sinclairiana* is most closely related

to *A. storkii*. These two species share erect, pilose pubescence of stems and floral structures. *Aphelandra sinclairiana* crosses readily with *A. terryae*, *A. golfodulcensis*, and *A. gracilis* (Table 11). Where geographic and elevational isolation break down, it hybridizes readily with the latter two species.

Additional specimens examined. COSTA RICA, CARTAGO: Atirro, 600 m, Donnell Smith 6694 (GH, US). LIMÓN: Río Valle Estrella drainage, Shank & Molina 4545 (F); Río Lari, Jimenez-M. 1916 (F, NY); along Río Sixaola, between Bribri and Bratsi, 10–50 m, Burger et al. 10420 (DUKE, F); Talamanca Valley, Carleton 124 (US).

PANAMA, BOCAS DEL TORO: vicinity of Chiriquí Lagoon, von Wedel 1083 (GH, MO, US); Changuinola, 30–60 m, Lewis et al. 803 (GH, MO, US); hillside above Almirante, Gentry 2684 (DUKE, F, MO). COCLÉ: vicinity of El Valle, 800–1,000 m, Allen 125 (A, F, MO); Bismark above Penonomé, Williams 370 (NY, US); El Copé, 250 m, McDaniel & Cooke 14831 (FSU, MO). COLÓN: edge of forest along Pipeline Road ca. 10 km NW of Gamboa, Wilbur & Teeri 13365 (DUKE, F), McDade 389 (DUKE); 8.7 mi. N of Río Chagres, along Boyd-Roosevelt Hwy., McDade 384 (DUKE); along Río Buenaventura near Portobelo, Kennedy & Gra 2239 (F, MO), McDade 289 (DUKE); W end of Gatún Lake Dam, Blum & Tyson 1975 (FSU, MO); between Fort Sherman and Gatún, 0–175 m, Burch et al. 1016 (F, MO, NY); Road S-10, N of Escobal, Croat 12443 (DUKE, F, MO). DARIÉN: Boca de Pauarando, on Sambú River, Pittier 5572 (NY). PANAMÁ: SE side of Madden Lake near Puente Natural, 90 m, Nee & Hansen 14047 (DUKE, MO, WIS); 5 mi. SW of Cerro Brewster, 1,000 ft., Lewis et al. 3316 (DUKE, F, MO, NY, US); Capiro, along trail between Lidice and Aguacate, 300 m, Foster 2140 (DUKE); Nuevo Emperador, Barrasco 28 (MO, PMA); slopes of Cerro Campana, 2,500–2,900 ft., Wilbur 24367 (DUKE).

3. *Aphelandra storkii* Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1197. 1938. TYPE: Costa Rica. Limon: Livingston, Río Reventazón, Rowles & Stork 690 (holotype, US).

Shrubs 1–3 m high, sparsely branched; stems terete, younger surfaces moderately pilose, the trichomes erect, white, about 1 mm long, older surfaces glabrate. Leaves opposite, obovate to broadly oblanceolate, 30–45 cm long, 15–20 cm wide, apically acuminate (the tip acute or blunt), basally long attenuate and decurrent on petiole, marginally entire to crenulate, sparsely strigose above, the trichomes appressed, white, about 0.75 mm long, moderately tomentose below, the trichome appressed, white, about 0.75 mm long, somewhat twisted, veins pilose, the trichomes erect, white, about 1 mm long; petioles 1–3 cm long, densely pilose, the trichomes erect, white,

about 1 mm long. Inflorescence terminal, spikes usually single (rarely 2–5), terete to subquadrangular, 15–25(–45) cm long, about 2 cm wide; peduncles 1–3 cm long (to 5 cm below lateral inflorescences), densely pilose, the trichomes erect, white, about 1 mm long; rachis densely pubescent, the trichomes erect, white, about 0.5 mm long; bracts imbricate, rhombic oblong-ovate, apically acute, marginally entire or bearing 2–3 minute teeth along each edge (each about 1 mm long and 0.25 mm wide), orange, 25–30 mm long, 13–18 mm wide, minutely puberulous within, moderately pubescent without, the trichomes appressed, white, about 0.5 mm long, margins ciliate, the trichomes white, about 1 mm long, the nectaries medial, composed of 10–15 individual glands, each about 0.5 mm long and 0.25 mm wide; bracteoles lanceolate, apically acute, 9–14 mm long, 2–4 mm wide, pale orange, moderately pubescent, the trichomes ascending, white, about 0.25 mm long. Sepals 13–17 mm long, apically acute, pale orange, striately nerved, moderately pubescent, the trichomes erect, white, about 0.25 mm long, the adaxial segment broadly lanceolate, 3.5–7 mm wide, the abaxial pair lanceolate, 2–4 mm wide, the lateral pair narrowly lanceolate, 1–2 mm wide; corolla orange, 6.5–7.5 cm long, moderately tomentose, the trichomes erect, white, about 0.5 mm long, frequently twisted, the tube 48–56 mm long, 4–5 mm in diameter at base, constricted to 2.5–3 mm above ovary (8 mm above base), expanding to 6–8 mm deep at throat, the upper lip erect, elliptic, 17–20 mm long, 10–15 mm wide, bilobed, the lobes triangular, acuminate, 8–11 mm long, anther pocket well-developed, the middle lobe of lower lip elliptic, 27–30 mm long, 9–12 mm wide, acute, the lateral lobes about 2 mm long and 5–6 mm wide; filaments inserted 9–10 mm from base of corolla tube, free portions about 5 cm long, the anthers 7–9 mm long, extending to within 5–6 mm of tip of upper lip, pollen orange; stigma very pale orange or uncolored, minutely bilobed, the style filiform, extending 1–7 mm beyond anthers, the ovary glabrous. Fruits clavate, terete, glabrous, green when immature, becoming black-brown at dehiscence, 28–32 mm long, about 7 mm wide, 5–6 mm thick; seeds brown, angularly orbicular, slightly flattened, 5–7 mm in diameter, 3–4 mm thick. Seed germination semi-hypogeal.

Habitat and distribution. This species is endemic to the Caribbean lowlands of northeastern

Costa Rica, occurring in forests with slight seasonal differences in rainfall [tropical wet to premontane wet forests (Holdridge, 1967)]. *Aphelandra storkii* is found in the understory of primary forest and in gaps of varying sizes, but rarely in extensively disturbed areas.

Flowering and fruiting. *Aphelandra storkii* flowers during the wettest months of the year (July through Nov.). Fruits are matured during the driest months of the year (Jan. to March).

This species may be readily distinguished from all other *Aphelandras* by the combination of monocaulous growth form and pilose pubescence of leaves and stems, distinctively colored floral bracts and corollas and large size of the bracts, calyx, and corolla. The few collections known of *A. storkii* show little morphological variability over its limited range.

Relationships. Among Central American species of Group I, *A. storkii* is most closely related to *A. sinclairiana*. It is a distinctive species with many uniquely derived character states. Closer relatives of this species may be found in South America. Among South American species, *A. grandis* Leonard, *A. aristei* Leonard, and *A. trianae* Leonard bear at least a superficial resemblance to *A. storkii* (Leonard, 1953).

Additional specimens examined. COSTA RICA. HEREDIA: past town of Pto. Viejo on road to Río Frío, 100 m, *McDade 232* (DUKE); Finca La Selva, along Río Pto. Viejo near town of Pto. Viejo, 100 m, *Grayum 2361* (DUKE), *McDade 350* (DUKE), *Opler 988* (F, MO), *Sperry 650* (DUKE), *Sperry 765* (DUKE), *Sperry 831* (DUKE), *Wilbur 33599* (DUKE); Río Bijagual, 2 km E of Tirimbina, *Maas 1324* (US).

4. *Aphelandra gracilis* Leonard, Proc. Biol. Soc. Wash. 56: 54. 1943. TYPE: Panama. Coclé: N of El Valle de Antón, 1,000 m, *Allen 2908* (holotype, US; isotypes, AAH, MO).

Shrubs or small trees, 2–7 m high, profusely branched; younger stems quadrangular, moderately pubescent, the trichomes upwardly appressed, white, 0.25–0.5 mm long, older stems terete, glabrate. Leaves opposite, elliptic to ovate, 10–20 cm long, 5–8 cm wide, apically acuminate (tip acute or blunt), basally acute or attenuate and decurrent on petiole, marginally entire, somewhat coriaceous and shiny, essentially glabrous above (few trichomes on veins), essentially glabrous below although sparsely pubescent on veins, the trichomes appressed, white, about 0.25 mm long; petioles 1–2 cm long, moderately pu-

bescent, the trichomes appressed, white, about 0.25 mm long. Inflorescences terminal, spikes solitary or 2–5, terete, 8–12(–15) cm long, about 1 cm wide, sessile; the rachis sparsely pubescent, the trichomes erect, white, about 0.25 mm long; bracts non-overlapping, internodes 7–10 mm long, bracts ovate, apically acute, marginally entire, 5–8 mm long, 3–4.5 mm wide, green, glabrous within, sparsely pubescent towards tip of midvein without, the trichomes appressed, white, about 0.25 mm long, margin sparsely and minutely ciliolate, the nectaries medial, composed of few (3–7) individual glands, each 0.5 mm in diameter; bracteoles narrowly ovate, apically acute, 4–6 mm long, 1.5–3 mm wide, green, essentially glabrous or with a few trichomes toward apex, these appressed, white, about 0.25 mm long. Sepals 7–9 mm long, apically acute, green, striate with narrow hyaline margins, essentially glabrous, the adaxial segment narrowly ovate, 2.5–4 mm wide, the abaxial pair lanceolate, 2–3 mm wide, the lateral pair narrowly lanceolate, 1–1.5 mm wide; corolla pink or orange-red, 6.5–7 cm long, minutely puberulous with erect trichomes, the tube 48–50 mm long, 3 mm in diameter at base, constricted to about 1.5 mm above ovary (5–7 mm above base), expanding to 8–10 mm deep at throat, the upper lip erect, ovate, 16–17 mm long, 9–12 mm wide, bilobed, the lobes triangular, apiculate, 6–9 mm long, anther pocket well-developed, the middle lobe of lower lip elliptic, 23–26 mm long, 8–10 mm wide, acute, the lateral lobes about 1 mm long, 5–6 mm wide; filaments inserted about 12 mm above base of corolla tube, free portion of each 4.3–4.6 cm long, the anthers 5–6 mm long, extending to within 4–6 mm from tip of upper lip, pollen cream-colored; stigma not distinctively colored, very minutely bilobed, the style filiform, extending 1–3 mm beyond anthers, the ovary glabrous. Capsules clavate, terete, green when immature, black at dehiscence, 20–22 mm long, about 6.5 mm wide and 4.5 mm thick; seeds brown, orbicular, slightly flattened, 3.5–5 mm in diameter, about 3 mm wide. Seed germination semi-hypogeal.

Habitat and distribution. *Aphelandra gracilis* is restricted to the provinces of Veraguas, Coclé, Colón and Panamá in central Panama (Fig. 56). It occurs from 700 to 1,200 m elevation in wet cloud forest habitat, and at lower elevations where local conditions combine to produce a wet, frequently fog-bound climate [Holdridge's (1976) premontane wet to premontane rain forests]. The

species is apparently limited to primary forest and is unable to survive in open areas.

Flowering and fruiting. Flowering occurs during the driest months of the year (late Dec. through early March), and fruits are matured during the late dry and early wet seasons.

Aphelandra gracilis is readily distinguished from all other *Aphelandras* treated here by its small green bracts that are distantly spaced along the rachis and its glabrous, slightly coriaceous and somewhat shiny leaves. Both field and herbarium studies suggest that hybridization between *A. gracilis* and *A. sinclairiana* occurs in areas where disturbed cloud forest habitats occur adjacent to seasonally dry low and premontane habitats on the Pacific slope of the central mountain range of Panama. Hybrids between these two species are quite vigorous and are intermediate in bract size, color, and spacing; leaf texture and pubescence; and overall plant pubescence. Collections of these hybrid plants have previously been identified as *A. gracilis*, *A. sinclairiana*, or the South American species *A. pilosa*. The misidentification of hybrid plants from El Llano (Panamá) as *A. pilosa* (Durkee, 1978) is readily understandable. These hybrids have the pubescence of *A. sinclairiana* (e.g., pilose stems), but much smaller bracts than are typical of this species, resulting in a superficial resemblance of these plants to *A. pilosa*.

Relationships. The bracteal nectaries, fruit and seed shape, and germination pattern of *A. gracilis* place it in Group I. Within Group I, its green bracts ally it with *A. golfodulcensis*, *A. panamensis*, and *A. deppeana*.

Additional specimens examined. PANAMA. COCLÉ: vicinity of El Valle de Antón, 700–1,200 m, Hunter & Allen 311 (US), Allen 1671 (F, GH, NY), Gentry & Dwyer 3587 (F, MO). COLÓN: Santa Rita Ridge, 200 m, Lewis et al. 5392 (MO), Mori & Kallunki 3025 (MO). PANAMÁ: 10 km above InterAm. Hwy. on road from El Llano to Cartí-Tupile, 150–350 m, Kennedy & Dressler 2954 (MO), Mori & Kallunki 2260 (MO); Cerro Jefe, about 10 km past Goofy Lake, 600 m, McDade 386 (DUKE), Nee 9291 (MO), Gentry et al. 3490 (MO), Gentry & Mori 13432 (F, MO), Wilbur et al. 11326 (DUKE); Gorgas Memorial Labs research camp, 5–10 km NE of Altos de Pacora, 600 m, Mori & Kallunki 3343 (MO); slopes of Cerro Campana, 800 m, Smith & Smith 3356 (F, US), Croat 22793 (F, MO, NY), Maas & Dressler 726 (MO). VERAGUAS: past Santa Fé, along road past Escuela Agrícola, slopes of Cerro Tute, 800–1,200 m, Croat 23038, 34200 (MO), Gentry 6247 (MO).

Putative hybrids between A. gracilis and A. sinclair-

iana. PANAMA. COCLÉ: vicinity of El Valle, 500–700 m, *Allen 1671*, 2300 (US), *Dwyer 11845* (MO), *Lewis et al. 2614* (MO). PANAMÁ: road from El Llano to Cartí-Tupile, 10–12 km above InterAm. Hwy., 200–500 m, *Nee et al. 8873* (MO), *Croat 22891* (MO).

5. *Aphelandra golfodulcensis* McDade, Ann. Missouri Bot. Gard. 69: 405. 1982 [1983].
TYPE: Costa Rica. San José: vicinity of El General, beside Río Chirripó, *Skutch 2573* (holotype, MO; isotypes, A, GH, NY, US).

Shrubs or small trees 1–6 m high, profusely branching; stems terete, younger stems densely pubescent, becoming moderate to sparse on older surfaces, the trichomes downwardly appressed, white, about 0.75 mm long. Leaves opposite (very rarely alternate), elliptic to oblanceolate, 25–30(–45) cm long, 12–15 cm wide, apically acute to acuminate (the tip acute or blunt), basally attenuate and decurrent on petiole, marginally entire or slightly undulate, upper surface essentially glabrous, sparsely pubescent on veins, the trichomes appressed, white, about 0.5 mm long, moderately pubescent below, the trichomes appressed (erect on veins), white, about 0.75 mm long; petioles to 1 cm long, moderately pubescent, the trichomes erect, white, about 0.5 mm long; leaves subtending inflorescences much reduced, 3–6 cm long, 1–2.5 cm wide, pubescence as of cauline leaves. Inflorescences terminal, spikes numerous, terete, 3–15 cm long, 0.75–1 cm wide, arranged in a freely branching panicle inflorescence; the peduncles 0.5–10 cm long, moderately pubescent, the trichomes erect to downwardly appressed, white, about 0.75 mm long; the rachis minutely puberulous, the trichomes erect, white; bracts imbricate, rhombic-ovate, apically acute, entire, 8–13 mm long, 4–7 mm wide, green to dull brown-orange, glabrous to sparsely papillate within, minute puberulous without, the trichomes appressed, white, margin ciliate, the trichomes white, about 0.25 mm long, the nectaries medial, composed of several (1–7) individual glands, each about 0.75 mm long and 0.5 mm wide; bracteoles narrowly ovate, apically attenuate, 4–6.5 mm long, 2–4 mm wide, green, moderately puberulous, the trichomes appressed, white. Sepals 6–9 mm long, apically acute, green, finely striate, minutely puberulous, the trichomes appressed, white, the adaxial segment narrowly ovate, 3–4 mm wide, the abaxial pair broadly lanceolate, 2–2.5 mm wide, the lateral pair narrowly lanceolate, about 1.5 mm wide; corolla orange to red, 6.3–7.3 cm long, minutely

puberulous, the trichomes erect, white, the tube about 4.7 cm long, 2–3 mm in diameter at base, slightly constricted above ovary (6 mm above base), expanding to 6–8 mm deep at throat, the upper lip erect, elliptic, 17–19 mm long, 7–11 mm wide, bilobed, the lobes triangular, acuminate, 6–10 mm long, anther pocket well-developed, the middle lobe of lower lip broadly lanceolate, 22–26 mm long, 6–9 mm wide, acuminate, the lateral lobes 1–3 mm long, 5–7 mm wide; filaments inserted about 15 mm above base of corolla tube, free portion of each about 4 cm long, the anthers 6–8 mm long, extending to within 5 mm from tip of upper lip, pollen very pale orange; stigma red, slightly bilobed, the lobes about 0.5 mm long, the style filiform, extending 3–5 mm beyond anthers, the ovary glabrous. Fruits clavate, terete, glabrous, green when immature, turning black-brown at dehiscence, 19–23 mm long, 5–8 mm wide, 5.5–7 mm thick. Seeds dark-brown, orbicular, slightly flattened, 4–6 mm in diameter, 2.5–3 mm wide. Seed germination semi-hypogeal.

Habitat and distribution. *Aphelandra golfodulcensis* is found primarily in the tropical wet forests (Holdridge, 1967) of the Golfo Dulce region of Puntarenas province, Costa Rica (Fig. 56). Its range extends into the adjacent Burica Peninsula of Panama (Chiriquí province), to mid-elevations above the Golfo Dulce region [premontane rain forests (Holdridge, 1967)], and to the north into Alajuela and Guanacaste provinces where local conditions result in a climate substantially wetter and less seasonal than is typical of these areas. The plants occur as understory shrubs in primary forests and also colonize successional and edge habitats.

Flowering and fruiting. Peak flowering occurs during the dry season (late Dec. through March). Fruits mature rapidly and few individuals still bear fruits when the wet season begins in this area.

Plants of *A. golfodulcensis* have previously been referred to *A. sinclairiana*. Morphological features distinguishing these two species include bract size, color, and pubescence; corolla tube vestiture; fruit color and pubescence; and overall vestiture of the plants. Data from artificial hybridizations support recognition of the two as distinct but closely related (Table 11). Several collections of putative hybrids between *A. golfodulcensis* and *A. sinclairiana* are known from

northeastern Costa Rica. These plants are sterile and are morphologically intermediate between the two parental species, most notably in vestiture of leaves, stems and corollas, and bract size and color.

Relationships. *Aphelandra golfodulcensis* is a member of Group I and is phylogenetically most closely related to *A. gracilis*, *A. panamensis*, and *A. deppeana* (Fig. 58).

Additional specimens examined. COSTA RICA. ALAJUELA: vicinity of Capulín on Río Grande de Tárcos, 80 m, *Standley 40160* (US); Santiago de San Ramón, *Brenes 6625* (A, F, NY). GUANACASTE: El Arenal, *Standley & Valerio 45105* (US). PUNTARENAS: ca. 10 km SE (toward Panama) of Palmar N. along InterAm. Hwy., *Burger & Matta-U. 4646* (F, MO, NY), *McDade 378* (DUKE); Esquinas forest, between Río Esquinas and Palmar S., *Allen 5775* (F, GH, US); Golfo Dulce and Río Térraba, *Skutch 5406* (F, US); forests of Santo Domingo de Golfo Dulce, *Tonduz 9969* (NY, US); Rincón de Osa, *Burger & Gentry 8851* (F); Sirena, Corcovado National Park, sea level, *McDade 401* (DUKE); Cañas Gordas, *Pittier 11193* (US); ca. 5 mi. from San Vito de Java, Las Cruces Botanical Garden, *McDade 395* (DUKE). SAN JOSÉ: Río Pacuar, vicinity of El General, *Skutch 3941* (MO, NY, US); Río Chirripó del Pacífico between Canaán and Chimiról, *Burger & Liesner 7117* (F, MO).

PANAMA. CHIRIQUÍ: Pto. Armuelles, 1 mi. W of airport, *Croat 21884* (F, MO, NY); ca. 2 mi. S of Pto. Armuelles, *Wilbur et al. 13583* (DUKE, F); San Bartolo Limite near Costa Rican border, 12 mi. W of Pto. Armuelles, 400–500 m, *Croat 22194* (DUKE, MO).

Putative hybrids between A. golfodulcensis and A. sinclairiana. COSTA RICA. HEREDIA: Finca La Selva, on Río Pto. Viejo near town of Pto. Viejo, 100 m, *McDade 367, 372* (DUKE). LIMÓN: Los Diamantes, Guapiles, 280 m, *Carpenter 373* (US), *Schubert 1109* (US), *Carlson 3457* (F, US); Llanos de Santa Clara, 650 ft., *Donnell Smith 4917* (GH, US); Santa Clara, Las Delicias, 500 m, *Biolley 10669* (US); Río Chirripó, hwy. from Río Frío to Guapiles, *Poveda 991* (F).

6. *Aphelandra panamensis* McDade, Ann. Missouri Bot. Gard. 69: 402. 1982 [1983]. TYPE: Panama. Panamá: slopes of Cerro Jefe, past Goofy Lake and large coffee finca, 800 m, *McDade 411* (holotype, DUKE; isotypes, F, MO).

Shrubs or small trees 1–6 m high, sparsely branched; stems terete, younger stems densely pubescent, the trichomes upwardly appressed, white, 0.5–0.75 mm long, older surfaces glabrate. Leaves opposite, narrowly elliptic, 15–18(–22) cm long, 3–6.5 cm wide, apically acuminate to acute, basally attenuate and decurrent on the petiole, marginally entire or undulate, the upper sur-

face of youngest leaves sparsely pubescent, glabrate with age, lower surface moderately pubescent, the trichomes appressed, white, about 0.5 mm long; petioles lacking or to 5 mm long, densely pubescent, the trichomes erect, white, about 0.5 mm long; uppermost leaves subtending inflorescences frequently reduced. Inflorescences terminal, spikes usually solitary (rarely to 5), terete, 4–12 cm long, 0.8–1.2 cm wide, sessile; the rachis densely pubescent, the trichomes erect, white, about 1 mm long; bracts slightly imbricate, narrowly rhombic-ovate, apically attenuate, marginally with 2–3 pairs of teeth (each 1–2 mm long), 11–15 mm long, 6–8 mm wide, green to pale dull orange, sparsely pubescent within, moderately pubescent without, the trichomes appressed, white, about 0.5 mm long, margins ciliate, the trichomes white, 0.25–0.5 mm long, the nectaries medial, composed of several (5–10) individual glands, each about 0.5 mm long and 0.3 mm wide; bracteoles lanceolate, apically acute, 6–10 mm long, 1.5–2.5 mm wide, straw-colored or green, glabrous except keel and apically sparsely pubescent, the trichomes erect, white, about 0.75 mm long. Sepals 8–12 mm long, apically acute, green or straw-colored, glabrous except for the sparsely pubescent tip, the trichomes erect, white, about 0.75 mm long, the adaxial segment narrowly ovate, 3–5 mm wide, the abaxial pair lanceolate, 2–3 mm wide, the lateral pair narrowly lanceolate, 1.5–2 mm wide; corolla bright red, 5.5–7 cm long, minutely puberulous except tip of lower lip sparsely pubescent, the tube about 5 cm long, 2.5–3 mm in diameter at base, constricted to 1.5 mm above ovary (about 8 mm above base), expanding to 5–7 mm deep at throat, the upper lip erect, elliptic, 14–20 mm long, 6–8 mm wide, bilobed, the lobes triangular, acute, 5–7 mm long, anther pocket poorly developed, the middle lobe of lower lip narrowly elliptic, 18–23 mm long, 4–7 mm wide, acute, tip strongly curled back toward tube, the lateral lobes about 0.5 mm long and 3 mm wide; filaments inserted about 5 mm above base of tube, free portion of each about 5 cm long, the anthers 4–5 mm long, extending to within 2–3 mm of tip of upper lip, pollen very pale yellow; stigma not distinctively colored, oblique and appearing hollow, the style filiform, extends 1–2 mm beyond anthers, the ovary glabrous. Fruits globose, terete, glabrous, green tinged with orange when immature, becoming yellow-brown at dehiscence, 16–19 mm long, 4.5–6.5 mm wide,

5.5–7 mm thick; seeds dark brown, irregularly orbicular, slightly flattened, 4–6 mm in diameter, 2–3 mm thick. Seed germination semi-hypogeal.

Habitat and distribution. *Aphelandra panamensis* is known only from central and eastern Panama in the provinces of Coclé, Colón, Panamá, San Blas, and Darién. It occurs in wet cloud forest habitats, predominantly above 600 m elevation, but occasionally lower where local climatic conditions result in high rainfall and frequent fog cover [Holdridge's (1967) premontane wet and premontane rain forests]. Individuals of this species are primarily understory shrubs of primary forest, but are found in advanced secondary forest as well.

Flowering and fruiting. Peak flowering occurs in the wet season (Sept. to Dec.) and fruits mature during the driest months of the year (late Dec. to early March). There is, however, considerable asynchrony among individuals at some sites. Notably, at Santa Rita Ridge, in the province of Colón, flowering individuals can be collected during most months.

The combination of toothed bracts with extrafloral nectaries and the 5.5–7 cm long corolla serve to distinguish *A. panamensis* from other species. Specimens of *A. panamensis* have previously been referred to *A. deppeana* from which it may be readily distinguished. The two species differ in habit, leaf vestiture, corolla length, and fruit size and color. They are found in different habitats and are pollinated by two distinct groups of hummingbirds.

Relationships. Within Group I, *A. panamensis* and *A. deppeana* are sister species, sharing toothed bracts, oblique stigmas, sub-globose fruits, and villous pubescence of the lower corolla lip. Artificial hybridizations indicate that *A. panamensis* crosses readily with all other species of Group I.

Additional specimens examined. PANAMA. COCLÉ: 8 km N of El Copé, near sawmill, 600–750 m, *Berg & Dressler* 2770 (US). COLÓN: ca. 7 mi. from Transisthm. Hwy., Santa Rita Ridge, *Wilbur et al.* 15078 (DUKE), *McDade* 283, 388 (DUKE), *Smith & Smith* 3433 (US). DARIÉN: S of El Real on slopes of Cerro Pirre, 500–1,000 m, *Foster & Kennedy* 1263 (DUKE), *McDade* 428 (DUKE). PANAMÁ: Cerro Jefe, about 8 km above Goofy Lake, 800 m, *Blum et al.* 1834 (FSU), *Foster & Kennedy* 1872 (DUKE, US), *Wilbur et al.* 11316 (DUKE), *Lewis et al.* 282 (DUKE, MO, US). SAN BLAS: between Río Diablo and Río Acuatí near Narganá, *Duke* 14887 (US).

7. *Aphelandra deppeana* Schldl. & Cham., *Linnaea* 5: 96. 1830. TYPE: Mexico. State not given, Hacienda de la Laguna, *Schiede & Deppe s.n.* (holotype, B, destroyed, not seen; F photo 8704 in US).

Aphelandra pectinata Nees in DC., *Prodr.* 11: 297. 1847. TYPE: Colombia. Department not given, Río Sinú, *Cuming* 1099 (lectotype, K, photo in US).

Aphelandra haenkeana Nees in DC., *Prodr.* 11: 298. 1847. TYPE: Mexico. Veracruz: Cordillera de Veracruz, *Galeotti* 909 (lectotype, US; isoelectotypes, K, P, W).

Aphelandra dukei Wassh., *Phytologia* 25: 475. 1973. TYPE: Panama. Panamá: Río Bayano, 1–4 mi. above Piria, 100 m, *Duke* 14397 (holotype, US; isotype, MO).

Shrubs 1–4 m high, profusely branched; youngest stems subquadrangular, moderately tomentose, the trichomes appressed, white, 0.75–1 mm long, twisted and somewhat matted, older stems terete, glabrate. Leaves opposite, elliptic, 15–22 cm long, (1.5–2–)5–8 cm wide, apically acute to short attenuate, basally attenuate and decurrent on petiole, marginally entire to undulate, both surfaces moderately tomentose (dense on veins below), the trichomes erect, white, 0.75–1 mm long, curling; petioles lacking or to 1 cm long, densely pubescent, the trichomes appressed, white, 0.5–0.75 mm long. Inflorescences terminal, spikes solitary or more frequently several (3–7), terete to sub-quadrangular, 8–12(–19) cm long, about 1 cm wide, sessile; the rachis moderately pubescent, the trichomes erect, white, about 0.5 mm long; bracts densely imbricate, broadly elliptic, apically long attenuate, marginally with 2–4 pairs of short teeth (1–2 mm long, 0.5 mm wide) on each side, 13–16 mm long, 6–8 mm wide, green to dull orange, glabrous within, moderately pubescent without, the trichomes appressed, white, about 0.5 mm long, margins ciliate, the trichomes 0.75–1 mm long; the nectaries medial, composed of several (2–5) individual glands, each about 1.25 mm long and 0.75 mm wide; bracteoles lanceolate, apically long attenuate and acute, 6–8.5 mm long, about 1.5 mm wide, green to pale orange, sparsely pubescent, the trichomes appressed, white, about 0.25 mm long. Sepals 8–9.5 mm long, apically acute, green to dull orange, glabrous except ciliate near apex, the trichomes white, about 1 mm long, the adaxial segment narrowly ovate, about 3 mm wide, the abaxial pair lanceolate, about 1.5 mm wide, the lateral pair narrowly lanceolate, about 1 mm wide; corolla pink, orange, or red, 36–41 mm

long, moderately pubescent, the trichomes erect, white, 0.25–0.5 mm long (except trichomes of lower lip 1 mm long), the tube 27–29 mm long, 2 mm in diameter at base, constricted to 1–1.5 mm wide above ovary (5 mm above base), expanding to 4–5 mm deep at throat, the upper lip erect, elliptic, 11–13 mm long, 5–6 mm wide, bilobed, the lobes triangular, 3–4 mm long, acute, anther pocket poorly developed, the middle lobe of lower lip narrowly oblong, strongly recurved at anthesis, 14–15 mm long, 3–4.5 mm wide; filaments inserted about 5 mm above base of corolla, free portion of each 2.5–2.7 cm long, the anthers 3–4 mm long, extending to within 2–4 mm from tip of upper lip, pollen cream or yellow; stigma not conspicuously colored, appears hollow, oblique at tip, the style filiform, extends 0.5–1.5 mm beyond anthers, the ovary glabrous. Capsules globose, terete, green when immature, turning brown-black at dehiscence, 13–17 mm long, 5–6 mm wide, 5–6.5 mm thick; seeds brown, orbicular, slightly flattened, 3.5–4.5 mm in diameter, 2–3 mm wide. Seed germination semi-hypogeal.

Habitat and distribution. Ranging from southern Mexico through Central America south to Bolivia and east to Surinam, *Aphelandra deppeana* is one of the most widely distributed species in the genus. It is the most xerophytic of the species treated here and is found primarily in seasonally dry lowland habitats [tropical dry to moist forests (Holdridge, 1967)], occasionally ranging to mid-elevations on leeward slopes. In Costa Rica and Panama, it is a common understory shrub in the seasonally deciduous forest and shrub communities of the Pacific lowlands and colonizes the disturbed secondary and edge habitats now common in these regions.

Flowering and fruiting. Flowering occurs primarily during the wet season (July through Dec.), with fruits maturing during the early dry season (Jan. through March). There is some variability among individuals at some sites and unusual individuals can be found in flower at most times of year.

This species is readily distinguished from all other Central American *Aphelandras* by the combination of short corollas (36–41 mm) and toothed bracts with extrafloral nectaries. Although there is some variability among collections from different areas of the range, especially

in leaf morphology, this species is remarkably uniform and is easily recognized.

Wasshausen (1973a) described *A. dukei* as a distinct species on the basis of its very narrow (1.5–2 cm) leaves. I consider *A. dukei* to be a morphological variant of *A. deppeana* unworthy of formal recognition for several reasons. No other morphological characters consistently separate the two; inflorescence characters are essentially uniform. Pollen grains of *A. dukei* are identical in size and ultrasculpturing to those of *A. deppeana*. The habitats of the two are identical and narrow-leaved plants are known only from within the range of *A. deppeana*. Narrow-leaved individuals have been collected from three locations in eastern Panama.

Relationships. Phylogenetic analysis indicates that *A. deppeana* and *A. panamensis* share several derived character states and are sister species. *Aphelandra deppeana* possess uniquely derived states of many characters, suggesting that it is a very divergent member of Group I. Crossing relationships corroborate this hypothesis: *A. deppeana* crossed readily only with its sister species, *A. panamensis* (Table 11).

The unique features of *Aphelandra deppeana* are perhaps related to its xerophytic habitat and weedy nature. Especially noteworthy are the short corollas that are apparently reduced from the 6–7 cm length considered primitive for this group. This change may have functional significance: long-billed hummingbirds do not generally occur in areas with harsh dry seasons. The only available hummingbird pollinators in such areas are species with relatively short bills.

Among South American species, comparative morphology suggests that *A. lasia* Leonard is the only close relative of *A. deppeana* (Leonard, 1953). Plants of this Colombian species are distinguished from *A. deppeana* by their longer corollas and larger and more densely pilose bracts with few, if any, minute teeth.

Additional specimens examined. MEXICO. CAMPECHE: beyond Hopalchen on Campeche-Mérida road, Moore 8078 (US). CHIAPAS: along road to El Sumidero, 9 km N of Tuxtla Gutierrez, 2,500 ft., Breedlove 13879 (US); 5.6 mi. SE of Chiapa de Corzo, along Hwy. 190, Shilom Ton 2950 (DUKE, US); 13 km N of Arriaga along Hwy. 195, 830 m, Breedlove 28299 (DUKE); along road from El Bosque to Simojovel, 3,000 ft., Shilom Ton 3076 (DUKE). GUERRERO: Hwy. 95, 5–6 mi. E of Acapulco, 400 ft., Carlson 3066 (DUKE, US); Vallecitos, Montes de Oca, 520 m, Hinton 9903 (US); vicinity of Acahuizotla between Chipalcingo and Acapulco, Moore 8124 (US); between Copala and Juchi-

tango, 200–600 ft., *Nelson* 2297 (US). OAXACA: Tehuantepec, Tapesco, S of Tres Cruces, 3,000 ft., *MacDougall* H56 (US); E of La Soledad, near Mitla, *Ernst* 2555 (US); Cerro de Cosolapa, Cosolapa, *Vera-Santos* 2617 (US); Tuxtepec, Chiltepec, and vicinity, 20 m, *Martinez-Calderón* 254 (US); Cerro Santo Domingo, district of Juchitan, 240 m, *Conzatti* 3735 (US). QUINTANA ROO: 36 km S of Dzuiche on Hwy. 164, 30 m, *Roe et al.* 1349 (US). VERACRUZ: Ciudad Alemán, Cosamaloapan, 10 m, *Martinez-Calderón s.n.* (US); along river draining Laguna de Catemaco, region of San Andres Tuxtla, *Dressler & Jones* 230 (US); Zacaupan and vicinity, *Purpus* 1938 (US). YUCATAN: Chichen Itza, *Rudd* 2033 (US); Uxmal, *Degener & Degener* 26785 (US); Coba, *Crockett* 150 (US); Progreso, *Steere* 3012 (US); vicinity of Chicheh, *Gaumer* 23798 (US).

GUATEMALA. ALTA VERAPAZ: near Pancajche, 900 m, *Standley* 91831 (US); Sacolal, 3,000 ft., *Turckheim* 825 (US); 1 km past Tucuru on road from Tactic to El Estos, 1,400 ft., *McDade* 211 (DUKE). CHIQUIMULA: between Esquipulas and Ataluapa, 800 m, *Molina & Molina* 25346 (US); 3 mi. SE of Quetzaltepeque, 1,200–1,500 m, *Steyermark* 31291 (US). ESCUINTLA: SE of Escuintla along Río Michatoya, 250–300 m, *Standley* 89138 (US); San Antonio Jute, 780 m, *Standley* 64901 (US); near San José, sea level, *Standley* 64076 (US). GUATEMALA: Sanarate, 810 m, *Kellerman* 6653 (US). HUEHUETENANGO: El Reposo, 900–1,000 m, *Williams et al.* 41247 (US); slopes above Río Selegua, 6,100 ft., *Harmon* 4801 (US). IZABAL: between Ceja and Cienaga, *Ortiz* 2299 (US); vicinity of Quirigua, 75–225 m, *Standley* 23910 (US). JALAPA: between Jalapa and San Pedro Pinula, 1,400–1,800 m, *Standley* 77087 (US). JUTIAPA: Jutiapa, 850 m, *Standley* 75121 (US). PETÉN: Parque Nacional de Tikal, *Tun Ortiz s.n.* (DUKE, US); Ceibal, 150 m, *Molina* 15861 (US); San Clemente de Dos Arroyos, *Bartlett* 12827 (US). QUETZALTENANGO: Colomba, 1,900 ft., *Skutch* 1370 (US). RETALHULEU: between Nueva Linda and Champerico, 120 m, *Standley* 87650 (US); Retalhuleu, *Kellerman* 6584 (US). SANTA ROSA: Llano Entero, SE of Chiquimulilla, 150 m, *Standley* 78737 (US); Guazacapán, 220 m, *Standley* 78702 (US); Jumaytepeque, 6,000 ft., *Donnell Smith* 4379 (US). SOLOLÁ: Patalul, 1,370 ft., *Donnell Smith* 154 (US). SUCHITEPEQUEZ: Patulul, 330–600 m, *Standley* 62184 (US). ZACAPA: above Teculután, 250–275 m, *Steyermark* 42150 (US); road between Zacapa and Chiquimula, 500–660 m, *Standley* 73849 (US).

BELIZE. BELIZE: Gracie Rock on Western Hwy., *Croat* 23905 (DUKE, US); Mt. Polo group, *Bartlett* 11349 (US). CAYO: 2–4 mi. SE of Georgeville along road to Augustine, *Sorensen* 7121 (US); N of Cayo, *Bartlett* 11947 (US); Mountain Pine Ridge, *Hunt* 42 (US); 47.2 mi. SW of Belize City on Western Hwy., *Ugent* 83 (WIS). COROZAL: San Antonio, *Lundell* 4969 (US). TOLEDO: Monkey River, Pine Ridge, *Gentle* 3774 (US).

EL SALVADOR. AHUACHAPÁN: Ahuachapán, 800–1,000 m, *Standley* 19893 (US). LA UNION: La Union, 150 m, *Standley* 20672 (US). MORAZÁN: N of Montecristo (NE of San Miguel), 200 m, *Tucker* 450 (US). SAN SALVADOR: Tonacatepeque, *Standley* 19440 (US). SAN VICENTE: San Vicente, 350–500 m, *Standley* 21220 (US). SONOSANTE: San Antonio del Monte, 250 m, *Standley* 22166 (US).

HONDURAS. COMAYAGUA: Siguatepeque, 1,100 m,

Williams & Williams 18475 (US). CORTÉS: San Pedro Sula, 1,000 ft., *Thieme* 5403 (US). EL PARAISO: road to Yuscarán, *Swallen* 11335 (US). MORAZÁN: Cerro de Uyuca, 900 m, *Morton* 7031 (US). SANTA BARBARA: Santa Barbara, 300 m, *Molina* 3669 (US).

NICARAGUA. CHINANDEGA: Chinandega, *Baker* 2057 (US). CHONTALES: Cuapa, *Marshall & Neill* 6675 (DUKE). ESTELÍ: Pueblo Nuevo, 600–700 m, *Williams & Molina* 42405 (US). MANAGUA: Rt. 1 km 17, Tipitapa, *Atwood* 2825 (WIS). MATAGALPA: 5–10 km W of Matagalpa, 600–700 m, *Williams et al.* 23801 (US). NUEVA SEGOVIA: Ocotal, *Hamblett* 802 (WIS). RIVAS: Ometepe Island, Lake Nicaragua, *Shimek & Smith* 146 (US); near Tola and Rivas, *White* 5354 (US).

COSTA RICA. ALAJUELA: Grecia, *Jimenez* 1142 (US); Turrubres near San Mateo, *Biolley* 7075 (US); Atenas, *Schubert & Madriz* 1036 (US). GUANACASTE: 5 mi. N of Cañas along InterAm. Hwy., 50 m, *McDade* 221, 377 (DUKE); Santa Rosa National Park, 30 km NW of Liberia, *Wilbur* 25092 (DUKE); Bahía el Coco and Sardinal, 0–150 m, *Burger & Baker* 9923 (DUKE); between Guayabo and Salitral, *Utley & Utley* 4009 (DUKE); Cabo Blanco Nature Preserve, southern tip of Nicoya Peninsula, 0–200 m, *Burger & Liesner* 6591 (US); 12 km E of Esparta on InterAm. Hwy., *Utley & Utley* 3644 (DUKE). PUNTARENAS: near Quepos and Río Naranjo, 20–150 m, *Burger et al.* 10543 (DUKE); ca. 10 mi. before Palmar N. on InterAm. Hwy. between Paso Real and Palmar N., *McDade* 290 (DUKE); 8 km NE of Buenos Aires, 600 m, *Wilbur* 25266 (DUKE); Las Cruces Botanical Garden, ca. 8 km from San Vito de Java, 1,200 m, *McDade* 396 (DUKE).

PANAMA. CHIRIQUÍ: 17 km NE of San Felix, new road to Cerro Colorado Copper Mines, 1,000 m, *Nee* 10680 (US); 12.4 mi. N of David, *Lewis et al.* 718 (US). COCLÉ: Ola, 100–350 m, *Pittier* 5036 (US); El Valle de Antón, 600 m, *Lewis et al.* 2595 (DUKE). DARIÉN: Punta Garachiné, *Duke* 10475 (US); Púculo, 70 m, *Mori & Gentry* 4245 (MO). HERRERA: between Las Minas and Pesé, *Oliver* 1349 (US); Ocu, *Stern et al.* 1738 (US). LOS SANTOS: vicinity of Tonosí, 117 ft., *Stern et al.* 1854 (US). PANAMÁ: Balboa, *Standley* 26047 (US); Paraiso, *Dwyer* 7143 (US); Fort Clayton, *Tyson & Blum* 3891 (FSU); 1 mi. SW of Cocoli, Rodman Naval Ammunition Depot, *Wilbur et al.* 12893 (DUKE, US); near Miraflores locks, *Croat* 12729 (DUKE); between Las Sabanas and Matias Hernandez, *Standley* 31911 (US); Taboguilla Island, *Miller* 1999 (US); Taboga Island, *Standley* 27864 (US); Río Bayano, 1–4 mi. above Piria, *Duke* 14397 (MO, US); road to El Valle de Antón, ca. km 18 from InterAm. Hwy., *Wilbur et al.* 1558 (DUKE); along InterAm. Hwy. near Jenine, Río Cañita, *Duke* 3840 (US). VERAGUAS: 11 km S of Santa Fé, 220 m, *Nee* 8153 (US); Soná, 500 m, *Allen* 1042 (US); 2 km NW of Atalaya, 100 m, *Nee* 8253 (US).

COLOMBIA. BOLÍVAR: San Martín de Loba, *Curran* 99 (US); Sincelejo, *Pennell* 4057 (US); vicinity of Cartagena, *Heriberto* 357 (US). BOYACÁ: San Antonio on Río Cusiari, 10 km above Maní, 250 m, *Haught* 2613 (US). META: San Juan de Arama, Río Guejar, 500 m, *Idrobo & Schultes* 1223 (US); 65 km E of Villavicencio, *Haught* 2501 (US); Los Llanos, La Venturoso on Río Meta, *Cuatrecasas* 4195 (US); Los Llanos, Río Casanare, Esmeralda, 130 m, *Cuatrecasas* 3816 (US). VAUPÉS: Cerro de Mitú, 380 m, *Cuatrecasas* 6878 (US). VICHADA: 10 km W of Las Gaviotas along road to Pto.

Gaitan, 180 m, *Davidse 5344* (US); 7 km NE of San José de Ocuné, 100 m, *Hermann 10973* (US).

VENEZUELA. AMAZONAS: Alto Orinoco, Salto Salas, *Croizat 513* (US); Alto Río Orinoco, 30 km above Santa Barbara, 125 m, *Maguire et al.* (US); 12.5 km S of Pto. Ayacucho, 230 m, *Davidse 2795* (US). ANZOÁTEGUI: on Caracas-Barcelona Hwy., 16 km E of Boca de Uchiré, *Gentry & Berry 14824* (US). APURE: bank of Río Meta, 19 km WSW of Paraquito, 75 m, *Davidse & Gonzalez 13973* (US). BOLÍVAR: 14 km SE of Caicara along Hwy. 19 to Cd Bolívar, 160 m, *Davidse 4338* (US). GUARICO: 14 km NWN of Altagracia de Orituco, road to Caucagera, 420 m, *Davidse 4160* (US). SUCRE: 7 km E of Mochima Hwy. between Cumaná and Pto. La Cruz, 250 m, *Davidse 5032* (US).

GUYANA. Maniparu Falls, *Atkinson 59* (US); junction of Mazaruni and Cuyuni Rivers, *Graham 336* (US); Ahyma, Demerara River above Wismar, *Hitchcock 17419* (US); SE of Georgetown, along coast, *Hitchcock 16916* (US).

SURINAM. Lower Saramacca River, Betti Creek, *Jonker-Verhoef & John 539* (US).

8. *Aphelandra lingua-bovis* Leonard, Contr. U.S. Natl. Herb. 31: 268. 1953. TYPE: Colombia. Chocó: La Concepción, 15 km E of Quibdó, 75 m, *Archer 2012* (holotype, US).

Shrubs 1–2 m high, very sparsely branched or more frequently unbranched; younger stems subquadrangular, moderately pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete and glabrate. Leaves opposite, elliptic to obovate, 20–35(–45) cm long, 11–17 cm wide, apically acuminate, basally acute to slightly attenuate, marginally entire to crenate, blades coriaceous, glabrous above, with few trichomes on veins, sparsely pubescent below (moderately on veins), the trichomes appressed, white, about 0.5 mm long; petioles 0.5–6 cm long, moderately pubescent, the trichomes appressed, white, about 0.5 mm long. Inflorescence terminal, spikes solitary (rarely 2–3), quadrangular, 20–35(–70) cm long, 1.2–1.5 cm wide; peduncle lacking or very rarely to 1 cm long, densely pubescent, the trichomes appressed, white, about 0.5 mm long; rachis sparsely pubescent, the trichomes erect, white, about 0.5 mm long; bracts closely fitting but not imbricate, 2–4 pairs of sterile bracts subtending spikes, floral bracts narrowly rhombic-ovate, apically attenuate and acute, entire, red-orange, 12–17 mm long, 7–11 mm wide, glabrous within, sparsely and minutely pubescent without, keel sometimes with a narrow band of trichomes, margin sub-hyaline, very finely ciliolate, the nectaries medial, about 2.5 mm long and 1–1.5 mm wide, composed of many

minute glands; bracteoles linear-lanceolate, apically acute, 11–17 mm long, 2–3.5 mm wide, pale orange, glabrous except keel densely pubescent, the trichomes erect, white, 0.5–0.75 mm long. Sepals 12–18 mm long, apically acute, pale orange, minutely puberulous except few longer trichomes near tips, these appressed, white, about 0.5 mm long, the adaxial segment narrowly ovate, 3.5–8 mm wide, the abaxial pair lanceolate, 2–3.5 mm wide, the lateral pair narrowly lanceolate, 1.5–2.5 mm wide; corolla red-orange or pink-orange, 5.5–6 cm long, minutely papillate, with few scattered trichomes, coriaceous, the tube 4–4.4 cm long, 3.5–5 mm wide at base, scarcely narrowed above ovary, expanding to about 6 mm deep at throat, the upper lip erect, broadly ovate, 10–12 mm long, 7–9 mm wide, bilobed, the lobes triangular, 2.5–3.5 mm long, minutely apiculate, anther pocket well-developed, the middle lobe of lower lip scarcely reflexed at anthesis, narrowly ovate, 15–17 mm long, 6–7 mm wide, minutely apiculate, the lateral lobes about 1 mm long, 4–5 mm wide; filaments inserted about 5 mm above base of tube, free portion of each about 40 mm long, the anthers 5–6.5 mm long, extending to within 2–5 mm of tip of upper lip, pollen light yellow; stigma not distinctively colored, minutely bilobed, the style filiform, extending 1–2 mm beyond anthers, the ovary glabrous. Fruits oblong, flattened, oval in cross-section, glabrous, orange-brown when immature, dark brown at dehiscence, 17.5–22 mm long, 5–6 mm wide, 3.5–5 mm thick; seeds brown, orbicular to somewhat angular in outline, flattened, 4–6.5 mm in diameter, 1.5–2 mm wide. Seed germination epigeal.

Habitat and distribution. *Aphelandra lingua-bovis* is a species of lowland, premontane and, more rarely, middle elevation forests (to 1,200 m) [tropical wet through lower montane rain forest (Holdridge, 1967)] from southern Costa Rica, through Panama to northern Colombia. The Panamanian distribution of this species is difficult to establish with certainty since collections from the entire Caribbean slope of that country are as yet very incomplete. The plants are understory sub-shrubs of wet forests that experience only a very short dry season, and are limited to minimally disturbed sites.

Flowering and fruiting. *Aphelandra lingua-bovis* flowers during the wettest months of the year (July through Nov.) and matures fruits during those months with least rainfall.

Individuals of this species may be identified by their diminutive size, narrowly rhombic-ovate floral bracts that are 12–17 mm long and apically attenuate, linear-lanceolate bracteoles, and relatively short corollas. There is considerable variation among specimens, especially with respect to leaf texture and bract size. Collections are as yet too few, however, to discern any geographic patterns of variability.

Costa Rican plants referred by Leonard (1938) to the Venezuelan species *A. micans* are properly placed in *A. lingua-bovis*. Leonard also reported collections of *A. micans* from Guatemala, but I have found no indication that *A. micans* occurs in Central America or that *A. lingua-bovis* ranges north of southwestern Costa Rica.

Relationships. The phylogenetic relationships of *A. lingua-bovis* remain incompletely resolved. Phylogenetic analysis placed it as the basal species of the Central American lineage sharing minute bracteal nectaries (Group II, Fig. 58). Artificial hybridizations and distribution patterns of the states of many characters, however, indicate that its relationships with this group are more distant than the interrelationships of the remaining five species. More closely related species probably occur in South America, including *A. garciae* Leonard, *A. longispica* Leonard, and *A. straminea* Leonard (Leonard, 1953).

Additional specimens examined. COSTA RICA. LIMÓN: Río Valle Estrella drainage, *Shank & Molina-R.* 4509 (F). PUNTARENAS: near Quepos and Río Naranjo, 20–150 m, *Burger et al.* 10627 (F); between Golfo Dulce and Río Térraba, 30 m, *Skutch* 5284 (F, US); ca. 10 km SE of Palmar N. along InterAm. Hwy., ca. 20 m, *Burger & Matta-U.* 4650 (DUKE, US); ca. 10 km E of Golfito, 50 m, *Lent* 424 (F, MO); Rincón de Osa, 20–300 m, *Liesner* 1883 (MO); vicinity of Tinoco station, between Río Esquinas and Palmar, 30 m, *Allen* 5477 (F, US); between Palmar N. and Pto. Cortez, 50 m, *Jimenez-M.* 2245 (F); Rincón de Osa, SW of airstrip, 20–60 m, *Utley & Utley* 1060 (DUKE); 5 km W of Rincón de Osa, 50–200 m, *Burger & Liesner* 7235 (F, MO, NY); near mi. 4 on camino al Pacífico W of Rincón de Osa, 30 m, *Raven* 21477 (F); Parque Nacional de Corcovado, sea level, *McDade* 402 (DUKE); between Agua Buena and San Vito de Java, 1,200 m, *Jimenez M.* 2452 (F); San Vito de Java, vicinity of Las Cruces Botanical Garden, 1,200 m, *Raven* 22017 (F, NY), *McDade* 442 (DUKE). SAN JOSÉ: low hills above Río Paquita, 5–50 m, *Dodge & Goerger* 9883 (F, MO).

PANAMA. COLÓN: Río Guanche, 1–4 km upstream from Portobelo road, 1–100 m, *Gentry* 8783 (MO), *Mori & Kallunki* 3009 (MO), *McDade* 287, 380 (DUKE); near bridge over Río Buenaventura, near Portobelo, sea level, *Foster & Kennedy* 1794 (DUKE), *McDade* 383 (DUKE). DARIÉN: ascent of Cerro Pirre

from Río Pirre S of El Real, 750–1,030 m, *Duke* 5329 (MO), *McDade* 429 (DUKE).

COLOMBIA. ANTIOQUIA: near Villa Arteaga, hwy. to sea, *Hodge* 7012 (F, US). BOYACÁ: Mt. Chapon, NW of Bogotá, extreme W part of Boyacá, *Lawrance* 18 (GH). CHOCÓ: Río Atrato, Tanando, 60 m, *Cuatrecasas & Llano* 24118 (US); Río Taparal off San Juan, 30 m, *Robinson* 229 (US); between La Oveja and Quibdó, *Archer* 1731 (US).

9. *Aphelandra leonardii* McDade, *Ann. Missouri Bot. Gard.* 69: 408. 1982 [1983]. TYPE: Panama. Panamá: Majé, about 5 mi. up Río Nuevo, a branch of Río Majé, *Foster & Kennedy* 1993 (holotype, DUKE; isotypes, F, MO).

Shrubs 1–5 m high, profusely branching; younger stems quadrangular, sparsely pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete, glabrate. Leaves opposite, obovate to elliptic, 10–20(–30) cm long, 4–10 cm wide, apically acuminate, basally acute to attenuate, marginally entire to slightly undulate, upper surface glabrous, lower surface glabrous to sparsely pubescent except veins sparsely to densely pubescent, the trichomes appressed, white, 0.5–0.75 mm long; petioles 0.3–1.5 cm long (rarely to 3 cm), sparsely pubescent, the trichomes appressed, white, about 0.5 mm long. Inflorescence terminal, spikes solitary to numerous, quadrangular, 3.5–14 cm long, 0.8–1 cm wide, sessile or rarely very short pedunculate; rachis sparsely pubescent, except frequently densely pubescent just below insertion point of each bract, the trichomes erect, white, about 0.5 mm long; 2–3 pairs of imbricate, densely pubescent sterile bracts borne below fertile bracts, the trichomes appressed, white, about 0.75 mm long; floral bracts barely imbricate, rhombic-ovate, apically acute, marginally entire, 7–10 mm long, 5–7 mm wide, green to bright orange, glabrous within, sparsely and minutely puberulous without, margin minutely ciliolate, the trichomes white, the nectaries medial, 2–3 mm long and 1–2 mm wide, composed of many minute glands (each ca. 0.1 mm in diameter); bracteoles lanceolate, apically attenuate, 6–9 mm long, 2–3 mm wide, green, finely striate, glabrous except densely pubescent on keel, the trichomes erect, white, about 0.5 mm long. Sepals 10–12 mm long, apically acute, yellow-green, finely striate, margins hyaline, essentially glabrous, the adaxial segment narrowly ovate, 3–5 mm wide, the abaxial pair lanceolate, about 3 mm wide, the lateral pair narrowly lanceolate, 1.5–2 mm wide; corolla

bright red, 6–7.3 cm long, essentially glabrous, the tube about 5 cm long, 4–5 mm in diameter at base, constricted to 1.5–2 mm above ovary (about 7 mm above base), expanding to 7–9 mm deep at throat, the upper lip erect, elliptic, 17–21 mm long, 8–10 mm wide, bilobed, the lobes triangular, acute, apiculate, 9–10 mm long, anther pocket well-developed, the middle lobe of lower lip narrowly ovate, strongly reflexed to lie along tube at anthesis, 21–28 mm long, 8–10 mm wide, acute, apiculate, the lateral lobes about 1 mm long and 6 mm wide; filaments inserted 8–11 mm from base of tube, free portion of each 4.5–5.3 cm long, the anthers 7–8 mm long, extending to within 4–6 mm from tip of upper lip, pollen yellow; stigma not distinctively colored, slightly bilobed, the lobes about 0.2 mm long, the style filiform, extends 1–6 mm beyond anthers, the ovary glabrous. Fruits oblong, flattened, oval in cross-section, glabrous, yellow-green when immature, yellow-brown at dehiscence, 17.5–19 mm long, about 5 mm wide, 3.5–4 mm thick; seeds brown, irregularly orbicular, strongly flattened, 3.5–6.5 mm in diameter, 1.5–2 mm thick. Seed germination epigeal.

Habitat and distribution. This species is known from lowland and premontane wet forests (Holdridge, 1967) in eastern Panama (Colón, Panamá, Darién, and San Blas), and from two localities in Costa Rica. Extensive collecting on the Caribbean slope of Panama will be required to firmly establish the range of this species. *Aphelandra leonardii* is a shrub of the forest understory and margins. The plants are found mostly in areas with little annual variation in rainfall, but a few collections have been made in seasonally dry areas.

Flowering and fruiting. Individuals of *A. leonardii* flower during the late wet season (Sept. to Dec.) and fruits mature during the driest months of the year (Jan. to April).

Individuals of this species may be distinguished from other Central American members of the *A. pulcherrima* complex by their shrubby habit, sessile, terminal clusters of inflorescences and small, rhombic-ovate and entire bracts. Specimens of this species were formerly referred to *A. pulcherrima* H.B.K. from which they differ most notably in the morphology of the bracteal nectaries. In *A. pulcherrima* the glands are few and large, whereas in *A. leonardii*, they are numerous, minute, and form a well-defined, oblong

patch on each side of the bract. The two species differ also in fruit and seed morphology, with terete capsules and sub-globose seeds present in *A. pulcherrima*, and strongly flattened capsules and seeds in *A. leonardii*. *Aphelandra pulcherrima* is wholly South American and appears to include at least three closely related species (contrast, for instance, the treatments of Leonard, 1953 and Wasshausen, 1975).

Although there is little morphological variability among the eastern Panama populations of this species, plants from Costa Rica are rather distinct in several features of vegetative morphology. Costa Rican plants are larger and more diffusely branched, and have leaves that are membranous, narrower (3–5 cm), and sparsely tomentose. With respect to inflorescence and floral characters, however, plants from the two regions are almost identical. The systematic significance of these differences is as yet unclear and will perhaps be clarified by further collections from intervening areas where the species is currently unknown. Although it is possible that collections from the two countries represent distinct species, data from interpopulation crosses (Table 10) support recognition of a single taxon.

Relationships. *Aphelandra leonardii* is a member of the lineage sharing bracteal nectaries of many minute glands (Group II). This group includes *A. laxa*, *A. campanensis*, *A. hartwegiana*, *A. darienensis*, and, provisionally, *A. lingua-bovis*. Excepting the last, problematic species, these share several derived character states including immediate opening of the corollas and pollen grains with unsculptured bands (Type II). Phylogenetic analysis indicates that *A. leonardii* is the sister group of the remaining four Central American members of this lineage (*A. laxa*, *A. campanensis*, *A. hartwegiana*, and *A. darienensis*).

Additional specimens examined. COSTA RICA. SAN JOSÉ: along Río Tarrazú between Frailes and San Andrés, 1,300 m, *Burger 4041* (DUKE, F, MO, NY). PROVINCE UNKNOWN: near Boca Culebra, Pacific coast (Puntarenas?), *Pittier 11988* (US).

PANAMA. COLÓN: forest along Río Indio de Gatún, sea level, *Maxon 4807* (NY, US); Río Providencia, 3 km SE of Achiote, 5–100 m, *Gentry & Nee 8652* (MO). Río Guanche, *D'Arcy 9696* (MO). DARIÉN: slopes of Cerro Pirre, 500–2,500 ft., *Duke & Elias E13889* (MO); summit camp between Sasardí and Mortí, 400 m, *Duke 10033* (MO); summit camp adjacent Darién-San Blas border along sea level canal route 17, 1,000–1,200 ft., *Oliver et al. 3676* (MO, US); between upper Río Membrillo and Camp 7 on the construction road to San

Blas, *Duke* 10865 (NY); Río Tucutí between Tucutí and Río Urogantí, *Duke* 5287 (MO); Río Aruza, *Bristan* 1248 (MO). PANAMÁ: along Río Chavaré above Chepo, 50–200 m, *Pittier* 4723 (US); along InterAm. Hwy. between El Llano and Río Mamóní, *Duke* 5631 (MO). SAN BLAS: along beach east of Pto. Obaldia, *Croat* 16890 (US); forest around Pto. Obaldia, *Pittier* 4280 (GH, NY, US); mainland opposite Ailigandí from mouth of Ailigandí River, *Lewis et al.* 172 (DUKE, MO, NY, US).

10. *Aphelandra laxa* Durkee, Ann. Missouri Bot. Gard. 65: 161. 1978. TYPE: Panama. San Blas: 15–20 km WSW of Pto. Obaldia on trail to Darién, Caribbean slope of cordillera, *Mori et al.* 6854 (holotype, MO).

Shrubs to 1.5 m high, sparsely branching; younger stems quadrangular, glabrous. Leaves opposite, ovate-elliptic, to about 35 cm long and 8.5 cm wide, apically acuminate, basally attenuate, marginally entire to undulate, glabrous above and below; petioles to about 4 cm long, glabrous. Inflorescences terminal, spikes solitary or few, sessile, to about 18 cm long and 0.5–1 cm wide; rachis glabrous; floral bracts non-overlapping, internodes 1.5–2 cm long, rhombic-ovate, apically acute, marginally entire, 7–10 mm long, 5–6 mm wide, glabrous within and without, margin minutely ciliate, the nectaries sub-medial, about 2 mm long and 0.75 mm wide, composed of many minute glands; bracteoles narrowly ovate, keeled, apically acute, 7–8 mm long, 2–2.5 mm wide, glabrous. Sepals 11–12 mm long, apically acute and apiculate, striately nerved, glabrous, the adaxial segment narrowly ovate, about 3.5 mm wide, the abaxial pair lanceolate, about 3 mm wide, the lateral pair lanceolate, 2–2.5 mm wide; corolla to about 7 cm long, red, minutely puberulous, the tube 42–46 mm long, about 4 mm in diameter at base, narrowed to 2 mm in diameter above ovary (3–4 mm above base), expanding to about 9 mm at throat, the upper lip erect, ovate, about 25 mm long and 8–10 mm wide, bilobed, the lobes triangular, about 11 mm long, acuminate, the middle lobe of lower lip narrowly ovate, 28–30 mm long, 9–11 mm wide, apically acute, the lateral lobes about 1 mm long and 6–7 mm wide; anthers 7–8 mm long, extending to tip of upper lip; stigma minutely bilobed, the style filiform, extending beyond anthers, the ovary glabrous. Fruits clavate, flattened, glabrous, about 16 mm long and 9 mm wide; seeds orbicular, strongly flattened, about 5 mm in diameter, 2.5 mm thick.

Habitat and distribution. This species is known only from the type specimen which is from eastern Panama in the province of San Blas. It is apparently found in wet forests of the Caribbean lowlands, but its range and habitat requirements cannot yet be delimited.

Flowering and fruiting. *Aphelandra laxa* apparently flowers and fruits during the wet season because the type specimen (collected in June) bore both flowers and capsules.

This species is distinguished from other Central American species of *Aphelandra* by its very large leaves, small bracts with minute glands, and elongated internodes between pairs of floral bracts.

Relationships. *Aphelandra laxa* is a member of Group II (species 8–13). Its leathery bracts and papillate corollas indicate that, among Central American species, it is the sister group of *A. campanensis*, *A. hartwegiana*, and *A. darienensis*.

Aphelandra laxa is known only from the type specimen.

11. *Aphelandra campanensis* Durkee, Ann. Missouri Bot. Gard. 65: 162. 1978. TYPE: Panama. Panamá: Cerro Campana, 1,000 m, *Croat* 12215 (holotype, MO; isotypes, DUKE, NY).

Shrubs 2–4 m high, sparsely branched; youngest stems quadrangular, moderately pubescent, the trichomes upwardly appressed, white, about 0.25 mm long, older stems terete, glabrate. Leaves opposite, elliptic to ovate, 20–30 cm long, 8–18 cm wide, apically acute to acuminate, basally acute to slightly attenuate, marginally entire to crenulate, glabrous above, sparsely pubescent below (denser on veins), the trichomes appressed, white, about 0.25 mm long; petioles 3–12 cm long, very narrow, moderately pubescent, the trichomes appressed and curling, white, about 0.25 mm long; leaves subtending inflorescence usually much reduced, 4–7 cm long, 2–4 cm wide, pubescence as of cauline leaves. Inflorescences terminal, spikes usually 1–3 (rarely 5 or more), quadrangular, 10–25 cm long, about 1.5 cm wide; peduncle lacking or to 1 cm long (longer below lateral inflorescences), essentially glabrous; rachis essentially glabrous; bracts barely imbricate, broadly rhombic-ovate, apically acute to slightly obtuse and apiculate, marginally entire, 11–14

mm long, 9–11 mm wide, deep red-orange, minutely puberulous within and without, keel moderately pubescent, the trichomes appressed, white, about 0.25 mm long, margin sub-hyaline, glabrous, the nectaries medial, 2–2.5 mm long and 1–1.5 mm wide, composed of many minute glands; bracteoles keeled and slightly falcate, apically acute, 11–13 mm long, 2–3 mm wide, pale orange, glabrous except densely pubescent on keel, the trichomes erect, white, 0.5–0.75 mm long. Sepals 15–18 mm long, apically obtuse and frequently minutely apiculate, pale orange, striate, glabrous, the adaxial segment narrowly oblong, 4–6.5 mm wide, the abaxial pair narrowly oblong, 3–4 mm wide, the lateral pair linear, 2–3 mm wide; corolla deep red-orange, 6–7 cm long, coriaceous, minutely puberulous and papillate; the tube 43–48 mm long, about 3 mm in diameter at base, slightly constricted above ovary (4–5 mm above base), expanding to 7–9 mm deep at throat, the upper lip erect, ovate, 17–20 mm long, 10–12 mm wide, bilobed, the lobes triangular, apiculate, 6–7 mm long, anther pocket well-developed, the middle lobe of lower lip elliptic, 22–25 mm long, 8–11 mm wide, acuminate and apiculate, strongly reflexed at anthesis to lie parallel to tube; filaments inserted about 7 mm above base of corolla, free portion of each 4.6–4.8 cm long, the anthers 8–9 mm long, extending to within 3–5 mm from tip of upper lip, pollen yellow; stigma minutely bilobed, pink, the style filiform, extends 2–4 mm beyond anthers, the ovary glabrous. Fruits oblong, flattened, oval in cross-section, green when immature, brown-black at dehiscence, 20–24 mm long, 6–8 mm wide, 5–6 mm thick; seeds brown, orbicular, strongly flattened, 4–6 mm in diameter, about 2 mm thick. Seed germination epigeal.

Habitat and distribution. *Aphelandra campanensis* is found predominantly at mid-elevations in central Panama in the provinces of Coclé, Panamá, Veraguas, and Colón, and in the Caribbean lowlands of western Panama (Bocas del Toro) and extreme southern Costa Rica (Limón). The distribution of *A. campanensis* is imperfectly known because only a few collections from the Caribbean lowlands of Panama have been made. Plants of this species occur in cloud forest habitat at mid-elevations and in wet lowland forests (Holdridge's premontane wet and premontane rain forests). The species grows in the forest understory, gaps, and disturbed, second-growth areas.

Flowering and fruiting. Peak flowering occurs during the mid wet season (Aug. through Nov.) and fruits mature late in the wet season and into the drier months of the year (Jan. and Feb.).

Aphelandra campanensis may be distinguished from most Central American species by its large, glabrous leaves, broadly rhombic-ovate bracts, bracteoles that are keeled and slightly falcate and calyx lobes that exceed the bracts. *Aphelandra hartwegiana* is similar in many respects but has strongly falcate bracteoles, larger and more ovate bracts that diverge from the rachis, longer calyx segments, and extremely coriaceous corollas.

There is some confusion about the identity of plants from the lowlands of western Bocas del Toro province. Collections from this region have been identified as *A. campanensis*, *A. crenata*, and *A. hartwegiana*. Part of the difficulty is due to the incomplete condition of some of the specimens in question. There is certainly variability among plants from this area, but I found that none of these specimens was outside of the range of variability encountered in *A. campanensis*. Until more collections are made and field and experimental studies carried out, these collections are best referred to *A. campanensis*.

Relationships. Phylogenetic analysis indicates that *A. campanensis*, *A. hartwegiana*, and *A. darienensis* are members of a monophyletic subgroup within Group II. The relationships of these species with other Central American members of the *A. pulcherrima* complex, and with South American species are discussed under *A. hartwegiana*.

Additional specimens examined. COSTA RICA. LIMÓN: between Cahuita and Bribri, 100 m, McDade 242 (DUKE); Toro Amarillo, Cantón de Pococí, Solís R. 443 (F).

PANAMA. BOCAS DEL TORO: hillside above Almirante, Gentry 2748 (MO, US); Water Valley, vicinity of Chiriquí Lagoon, von Wedel 1428 (GH, MO); Pumpkin River, vicinity of Chiriquí Lagoon, von Wedel 2589 (GH, US). COCLÉ: El Copé, 250 m, McDade 531 (DUKE); vicinity of El Valle and Cerro Pilon, 700–900 m, Gentry & Dwyer 3665 (MO, NY), Luteyn & Kennedy 1683 (DUKE, F, MO), McDade 273, 441 (DUKE). COLÓN: around Dos Bocas, Río Fato valley, 40–80 m, Pittier 4195 (NY, US). PANAMÁ: Cerro Campana, ca. 900 m, Porter et al. 4966 (MO, US), McDade 279 (DUKE), Lewis et al. 3059 (US); 25 km NE of Cerro Azul on Río Piedras, 550 m, Mori & Kallunki 3284 (MO). VERAGUAS: valley of Río Dos Bocas on road between Alto Piedra and Calovébora, 350–400

m, Croat 27356 (MO); ca. 5 mi. past Santa Fé on road past Agricultural School, 700 m, McDade 268 (DUKE).

12. *Aphelandra hartwegiana* Nees ex Benth., Pl. Hartw. 236. 1846. TYPE: Colombia. Cundinamarca: Hacienda de Palmar, near Guaduas, Hartweg 1270 (holotype, K, not seen).

Shrubs 1–4 m high, sparsely branched; younger stems subquadrangular, sparsely pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete, glabrate. Leaves opposite, broadly elliptic, 25–40 cm long, 10–15 cm wide, apically acute to slightly acuminate, basally acute or attenuate, marginally entire, undulate or crenate, essentially glabrous above, sparsely pubescent below (moderate on veins), the trichomes appressed, white, 0.25–0.5 mm long; petioles 1–4 cm long, moderately pubescent, the trichomes appressed, white, 0.25–0.5 mm long; leaves reduced in size towards inflorescence. Inflorescences terminal, spikes solitary (rarely 2–5), subquadrangular, 15–30(–40) cm long, 1.5–2 cm wide; peduncles 0.5–1.5 cm long (longer below lateral inflorescences), sparsely pubescent, the trichomes appressed, white, about 0.25 mm long; rachis glabrous; 3–5 pairs of sterile bracts subtend spikes; floral bracts imbricate, broadly ovate, apically obtuse, entire, 13–16 mm long, 11–14 mm wide, deep orange, striate, essentially glabrous within and without, the nectaries supra-medial, 3.5–4.5 mm long and 2–2.5 mm wide, composed of many minute glands; bracteoles falcate, keeled, apically acute, 7–10 mm long, 3–5 mm wide, orange, glabrous or sparsely pubescent on keel, the trichomes appressed, white, about 0.5 mm long. Sepals 17–22 mm long, orange, frequently fading to white toward base, striate, glabrous or with a few trichomes toward apex, the adaxial segment oblong, apically obtuse, 6–9 mm wide, the abaxial pair narrowly oblong, apically acute, 4–5.5 mm wide, the lateral pair narrowly oblong, apically acute, 3–4 mm wide; corolla 6.5–7 cm long, yellow (infrequently orange), glabrous, very coriaceous, the tube 44–48 mm long, about 4 mm in diameter at base, narrowed to about 3 mm above ovary (about 7 mm above base), expanding to 8–9 mm deep at throat, the upper lip erect, ovate, 20–22 mm long, 11–13 mm wide, bilobed, the lobes triangular, 9–12 mm long, anther pocket very well-developed, the middle lobe of lower lip elliptic, about 25 mm long and 12 mm wide, apically acute, the lateral lobes about 1 mm long

and 5 mm wide; filaments inserted about 7 mm above base of corolla tube, free portion of each 4.2–4.6 cm long, the anthers 9–10 mm long, extending to within 3–5 mm from tip of upper lip, pollen yellow; stigma not distinctively colored, minutely bilobed, the style filiform, extending 3–5 mm beyond anthers, the ovary glabrous. Fruits clavate, flattened, oval in cross-section, green when immature, turning brown-black at dehiscence, 28–31 mm long, 7–8.5 mm wide, 5–7 mm thick; seeds brown, orbicular, strongly flattened, 5–7 mm in diameter, about 2 mm thick. Seed germination epigeal.

Habitat and distribution. *Aphelandra hartwegiana* is found in the lowlands of eastern Panama and northern Colombia. It is a species of wet forests with mild dry seasons (or essentially aseasonal precipitation) [Holdridge's (1967) tropical wet forest]. The plants grow in gaps in the forest, very frequently along streams, trails and clearings, and in extensive secondary areas.

Flowering and fruiting. Peak flowering occurs during the wettest months of the year (Aug. through Nov.), with fruits maturing during the drier months of Jan. through March.

The large, broadly ovate bracts, strongly falcate bracteoles, 2 cm long calyx lobes, and extremely coriaceous, yellow corolla readily distinguish this species from all other Central American *Aphelandras*. Specimens of *A. hartwegiana* show a definite decrease in bract size from west to east. The systematic significance of this apparently very gradual, clinal variation is as yet unclear. Collections are quite few and I have not been able to study Colombian plants in the field.

A single collection from the Darién (Allen 5094) of Panama was identified as the South American species *A. crenata* by Durkee (1978). I found this specimen to be within the range of variability encountered in collections of *A. hartwegiana* from this region, but recognize the need for further study of these two species, especially in light of the clinal decrease in bract size of *A. hartwegiana* that results in Panamanian specimens at least superficially similar to *A. crenata*.

Relationships. Among the species treated here, *A. hartwegiana* is a member of Group II and is most closely related to *A. campanensis* and *A. darienensis*. *Aphelandra hartwegiana* and *A. campanensis* are also similar to the South American species *A. crenata* Leonard and *A.*

chaponensis Leonard (Leonard, 1953; Durkee, 1978). These four species are similar in a number of morphological features including habit; large, essentially glabrous leaves that are frequently marginally crenate; broadly ovate floral bracts; sepals markedly longer than the bracts; and falcate bracteoles. Elucidation of the phylogenetic relationships among these species will require further study of the South American species.

Additional specimens examined. PANAMA. DARIÉN: Cocalito, Pacific coast near Darién-Colombia border, Dwyer 4339 (MO); along Sambú River, southern Darién, sea level, Pittier 5557 (US); vicinity of Pinogana, 20 m, Allen 921 (NY, US); trail between Pinogana and Yaviza, 15 m, Allen 257 (A, GH); Río Chico, vicinity of Yaviza, 10 m, Allen 5094 (MO); vicinity of Paya, Río Paya trail between Paya and Payita, Stern *et al.* 177 (US); S of El Real, headwaters of Río Pirre, ca. 100 m, Foster & Kennedy 1247 (DUKE), McDade 425 (DUKE); Río Tacarcuna, vicinity of old Tacarcuna village, 580 m, Gentry & Mori 13583 (MO). SAN BLAS: mainland opposite Ailigandí, Lewis *et al.* 191 (US).

COLOMBIA. ANTIOQUIA: near Villa Arteaga on hwy. to sea, 150 m, Hodge 7053 (US); near Chigoradó, 40 km S of Turbo, 50 m, Haught 4699 (US); Uraba, Mutatá, 100 m, Uribe 1505 (US); between Villa Arteaga and Chigoradó at Lomitas, Cuatrecasas & Willard 26108 (US). BOLÍVAR: Boca Verde on Río Sinú, Pennell 4580 (NY). CHOCÓ: Río Atrato, Quibdó, 40 m, Forero *et al.* 1451 (MO); mouth of Río Truando, Castaneda 4669 (NY); Pacific coast, Cupica, Fernandez 354 (US); Bahía Solano, along Quebrada Jellita, 50–100 m, Killip & Garcia 35639 (US); Río Chintado, above La Nueva, Duke 9863 (US).

13. *Aphelandra darienensis* Wassh., Phytologia 25: 480. 1973. TYPE: Panama. Darién: Cerro Pirre, 750–1,350 m, Duke & Elias 13756 (holotype, US; isotype, MO).

Shrubs 1–4 m high, sparsely branching; younger stems subquadrangular, sparsely pubescent, the trichomes upwardly appressed, white, about 0.5 mm long, older stems terete, glabrate, stems very thick and almost succulent. Leaves opposite, broadly elliptic, 25–35(–45) cm long, 10–17(–20) cm wide, apically acute, basally acute, marginally entire to crenulate, essentially glabrous to very sparsely pubescent above, the trichomes appressed, white, 0.75–1 mm long, sparsely pubescent below (except moderate on veins), the trichomes appressed, white, 0.5–0.75 mm long; petioles 3–9 cm long, moderately pubescent, the trichomes appressed, white, 0.75–1 mm long. Inflorescences terminal, spikes solitary (rarely 2–3), 10–18 cm long, 2.5–3 cm wide, sessile; rachis essentially glabrous; lower 1–3 pairs

of bracts leaf-like and sterile; floral bracts densely imbricate, ovate, apically obtuse and arching away from rachis, entire, frequently notched at apex, 30–40 mm long, 18–26 mm wide, deep orange, very leathery-coriaceous, sparsely puberulous within and without, with few scattered longer (about 1 mm) trichomes, the nectaries medial, 3–4.5 mm long and 1–2 mm wide, composed of many minute glands; bracteoles slightly falcate, apically acute, 9.5–13 mm long, 4–6 mm wide, pale orange, essentially glabrous. Sepals 15–18 mm long, apically acute, dull orange, essentially glabrous or with few scattered trichomes, the adaxial segment broadly elliptic, 8.5–9 mm wide, the abaxial pair elliptic, about 5 mm wide, the lateral pair lanceolate, 3.5–4 mm wide; corolla orange, minutely papillate, 6.8–7.2 cm long, coriaceous, the tube 48–49 mm long, about 5 mm in diameter at base, narrowed to about 3 mm above ovary (about 6 mm above base), expanding to about 7 mm deep at throat, the upper lip erect, oblong, 18–20 mm long, 11–13 mm wide, bilobed, the lobes triangular, about 8 mm long, 11–13 mm wide, apically emarginate and apiculate, anther pocket well-developed, the middle lobe of lower lip ovate, 27–29 mm long, 10–12 mm wide, apically obtuse, the lateral lobes 2–2.5 mm long and 7 mm wide; filaments inserted about 8 mm above base of corolla tube, free portion of each 4.7–4.8 cm long, the anthers 8–9 mm long, extending to within 5–6 mm from tip of upper lip, pollen yellow; stigma orange, bilobed, the lobes about 0.2 mm long, style filiform, extending about 5 mm beyond anthers, the ovary glabrous. Fruits elliptic, flattened, oval in cross-section, green when immature, black at dehiscence, about 35 mm long, 8.5–9.5 mm wide, about 5 mm thick; seeds dark brown, strongly flattened, about 9 mm in diameter and 2–2.5 mm wide. Seed germination epigeal.

Habitat and distribution. *Aphelandra darienensis* is apparently endemic to the mountains of the Darién in eastern Panama. It is restricted to mid-elevation cloud forest habitats and occurs only in primary forest [lower montane rain forest (Holdridge, 1967)].

Flowering and fruiting. Flowering occurs during the early wet season (July through Sept.) and fruits mature during the remainder of the wet season (through Dec.). Data on seasonality of reproduction are rather tentative because collections of this species are still quite few.

Aphelandra darienensis is extremely distinctive and is readily identified from flowering or fruiting material. Most characteristic are the large (to 40 mm), leathery and strongly recurved floral bracts. The extremely large leaves and thick, almost succulent stems, as well as the unique apical shape of the upper corolla lip lobes (emarginate and apiculate), and very long capsules also distinguish the species.

Relationships. The results of phylogenetic analysis indicate that this species is a member of the lineage including the other Central American species with minute glands (Group II). Within this group, closest relatives are *A. hartwegiana* and *A. campanensis*. Wasshausen (1973a) suggests a relationship based on morphological similarity with *A. fernandezii* Leonard, a Colombian species that bears at least a superficial resemblance to *A. darienensis*. Further study of South American members of the *A. pulcherrima* complex will be necessary to satisfactorily resolve the phylogenetic relationships of this unusual species.

Additional specimens examined. PANAMA, DARIÉN: W slope of Cerro Pirre, 2,500–4,500 ft., *Duke 6101* (MO), *McDade 430* (DUKE); between Tres Bocas and Cerro Campamiento on Cuasi-Caña trail, *Kirkbride & Duke 1350* (MO); Cerro Campamiento, S of Cerro Pirre, *Duke 15620* (US).

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APPENDIX A. Members of the *Aphelandra pulcherrima* complex.

<i>A. albert-smithii</i> Leonard	<i>A. leonardii</i> McDade
<i>A. aristei</i> Leonard	<i>A. lingua-bovis</i> Leonard
<i>A. attenuata</i> Wassh.	<i>A. macrophylla</i> Leonard
<i>A. barkleyi</i> Leonard	<i>A. macrostachya</i> Nees
<i>A. blandii</i> Lindau	<i>A. micans</i> Moritz ex Vatke
<i>A. campanensis</i> Durkee	<i>A. mildbraediana</i> Leonard
<i>A. chaponensis</i> Leonard	<i>A. panamensis</i> McDade
<i>A. crenata</i> Leonard	<i>A. parvispica</i> Leonard
<i>A. darienensis</i> Wassh.	<i>A. pharangophila</i> Leonard
<i>A. deppeana</i> Schldl. & Cham.	<i>A. pilosa</i> Leonard
<i>A. dielsii</i> Mildbr.	<i>A. pulcherrima</i> (Jacq.) H.B.K.
<i>A. fasciculata</i> Wassh.	<i>A. schieferae</i> Leonard
<i>A. fernandezii</i> Leonard	<i>A. scolnikae</i> Leonard
<i>A. garciae</i> Leonard	<i>A. sericantha</i> Leonard
<i>A. golfodulcensis</i> McDade	<i>A. sinclairiana</i> Nees
<i>A. gracilis</i> Leonard	<i>A. storkii</i> Leonard
<i>A. grandis</i> Leonard	<i>A. straminea</i> Leonard
<i>A. hartwegiana</i> Nees ex Benth.	<i>A. taborensis</i> Leonard
<i>A. haughtii</i> Leonard	<i>A. terryae</i> Standley
<i>A. lasia</i> Leonard	<i>A. tetragona</i> (Vahl) Nees
<i>A. laxa</i> Durkee	<i>A. trianae</i> Leonard
	<i>A. xanthantha</i> Leonard

APPENDIX B. Sources of pollen for size analysis (LW) and scanning electron microscopy study (SEM).

Collector and Number	Location	Used for
1. <i>A. terryae</i>		
Lewis et al. 126 (US)	Achituppu, San Blas, Pan.	LW
Tyson et al. 3815 (DUKE)	Cerro Piriaque, Darién, Pan.	LW
Haught 2098 (US)	Santander, Col.	LW
Duke 5187 (MO)	Río Pirre, Darién, Pan.	LW
McDade 431 (DUKE)	Río Pirre, Darién, Pan.	SEM/LW
Gentry & Mori 13550 (MO)	Pucuro, Darién, Pan.	LW
2. <i>A. sinclairiana</i>		
Donnell-Smith 6694 (US)	Atirro, Cartago, C.R.	LW
Wilbur et al. 13365 (DUKE)	Colón, Pan.	LW
McDade 280 (DUKE)	Colón, Pan.	SEM/LW
McDade 384 (DUKE)	Portobelo, Colón, Pan.	SEM/LW
Burger et al. 1977 (F)	Bribri, Limón, C.R.	LW
McDaniel & Cooke 14831 (FSU)	El Copé, Coclé, Pan.	LW
McDade 532 (DUKE)	El Copé, Coclé, Pan.	SEM/LW
Hunter & Allen 358 (MO)	El Valle, Coclé, Pan.	LW
McDade 528 (DUKE)	El Valle, Coclé, Pan.	SEM/LW
Pittier 5572 (NY)	Sambú River, Darién, Pan.	LW
Von Wedel 973 (MO)	Bocas del Toro, Pan.	LW
3. <i>A. storkii</i>		
McDade 350 (DUKE)	Pto. Viejo, Heredia, C.R.	SEM/LW

APPENDIX B. Continued.

Collector and Number	Location	Used for
4. <i>A. gracilis</i>		
<i>Nee</i> 9291 (MO)	Cerro Jefe, Panamá, Pan.	LW
<i>McDade</i> 421 (DUKE)	Cerro Jefe, Panamá, Pan.	SEM/LW
<i>Lewis et al.</i> 5392 (MO)	Sta. Rita Ridge, Colón, Pan.	LW
<i>Mori & Kallunki</i> 1801 (MO)	Sta. Rita Ridge, Colón, Pan.	LW
<i>Allen</i> 1671 (US)	El Valle, Coclé, Pan.	LW
<i>McDade</i> 529 (DUKE)	El Valle, Coclé, Pan.	SEM/LW
<i>Kennedy & Dressler</i> 2954 (MO)	El Llano, Panamá, Pan.	LW
<i>Croat</i> 22793 (F)	Cerro Campana, Panamá, Pan.	LW
5. <i>A. golfodulcensis</i>		
<i>Skutch</i> 3941 (US)	El General, San José, C.R.	LW
<i>McDade</i> 378 (DUKE)	Palmar, Puntarenas, C.R.	SEM/LW
<i>McDade</i> 401 (DUKE)	Corcovado, Puntarenas, C.R.	SEM/LW
<i>Croat</i> 21884 (F)	Pto. Armuelles, Chiriquí, Pan.	LW
<i>Pittier & Biolley</i> 7072 (US)	San Mateo, San José, C.R.	LW
<i>Allen</i> 5775 (US)	Esquinas, Puntarenas, C.R.	LW
<i>Liesner</i> 389 (MO)	Burica, Chiriquí, Pan.	LW
<i>McDade</i> 251 (DUKE)	San Vito, Puntarenas, C.R.	SEM/LW
6. <i>A. panamensis</i>		
<i>Foster & Kennedy</i> 1872 (DUKE)	Cerro Jefe, Panamá, Pan.	LW
<i>McDade</i> 411 (DUKE)	Cerro Jefe, Panamá, Pan.	SEM/LW
<i>Foster & Kennedy</i> 1263 (DUKE)	Cerro Pirre, Panamá, Pan.	LW
<i>McDade</i> 428 (DUKE)	Cerro Pirre, Panamá, Pan.	SEM/LW
<i>McDade</i> 284 (DUKE)	Sta. Rita Ridge, Colón, Pan.	SEM/LW
7. <i>A. deppeana</i>		
<i>Ton</i> 3076 (DUKE)	Chiapo de Corzo, Chiapas, Mex.	LW
<i>McDade</i> 377 (DUKE)	Cañas, Guanacaste, C.R.	SEM/LW
<i>McDade</i> 252 (DUKE)	San Vito, Puntarenas, C.R.	SEM/LW
<i>McDade</i> 290 (DUKE)	Palmar, Puntarenas, C.R.	SEM/LW
<i>Ortiz s.n.</i> (DUKE)	Tikal, El Petén, Guat.	LW
<i>McDade</i> 533 (DUKE)	El Copé, Coclé, Pan.	SEM/LW
<i>McDade</i> 530 (DUKE)	El Valle, Coclé, Pan.	SEM/LW
<i>A. dukei</i> (= <i>A. deppeana</i>)		
<i>Duke</i> 14397 (US)	Piria, Panamá, Pan.	LW
<i>Mori & Gentry</i> 4245 (MO)	Pucuro, Darién, Pan.	SEM/LW
8. <i>A. lingua-bovis</i>		
<i>Archer</i> 2012 (US)	Chocó, Col.	SEM/LW
<i>Skutch</i> 5284 (US)	Golfo Dulce, Puntarenas, C.R.	LW
<i>McDade</i> 399 (DUKE)	Corcovado, Puntarenas, C.R.	SEM/LW
<i>Allen</i> 924 (GH)	Pinogana, Darién, Pan.	LW
<i>McDade</i> 429 (DUKE)	Río Pirre, Darién, Pan.	SEM/LW
<i>McDade</i> 442 (DUKE)	San Vito, Puntarenas, C.R.	SEM/LW
9. <i>A. leonardii</i>		
<i>Duke et al.</i> 3611 (US)	Cerro Diablo, San Blas, Pan.	LW
<i>Foster</i> 1996 (F)	Majé, Panamá, Pan.	LW
<i>Lewis et al.</i> 172 (DUKE)	Ailigandí, San Blas, Pan.	LW
<i>D'Arcy</i> 9696 (MO)	Portobelo, Colón, Pan.	LW
<i>McDade</i> 310 (DUKE)	Frailes, San José, C.R.	SEM/LW
<i>Pittier</i> 11988 (US)	Boca Culebra, San José, C.R.	LW
<i>McDade</i> 432 (DUKE)	Cerro Pirre, Darién, Pan.	SEM/LW

APPENDIX B. Continued.

Collector and Number	Location	Used for
10. <i>A. laxa</i>		
<i>Mori et al.</i> 6854 (MO)	Pto. Obaldia, San Blas, Pan.	SEM/LW
11. <i>A. campanensis</i>		
<i>Weaver</i> 1648 (DUKE)	El Valle, Coclé, Pan.	LW
<i>McDade</i> 271 (DUKE)	El Valle, Coclé, Pan.	SEM/LW
<i>Von Wedel</i> 1428 (GH)	Chiriquí Lagoon, Bocas del Toro, Pan.	LW
<i>McDade</i> 242 (DUKE)	Bribri, Limón, C.R.	SEM/LW
<i>McDade</i> 531 (DUKE)	El Copé, Panamá, Pan.	SEM/LW
12. <i>A. hartwegiana</i>		
<i>Allen</i> 921 (US)	Pinogana, Darién, Pan.	LW
<i>McDade</i> 425 (DUKE)	Rio Pirre, Darién, Pan.	SEM/LW
<i>Cuatrecasas</i> 26108 (US)	Antioquia, Col.	LW
<i>Lewis et al.</i> 191 (US)	Ailigandí, San Blas, Pan.	LW
13. <i>A. darienensis</i>		
<i>Duke & Elias</i> 13756 (US)	Cerro Pirre, Darién, Pan.	LW
<i>McDade</i> 430 (DUKE)	Cerro Pirre, Darién, Pan.	SEM/LW
<i>A. pulcherrima</i>		
<i>Blum</i> 3523 (US)	La Popé, Bolívar, Col.	SEM
<i>Killip & Smith</i> 14516 (US)	Arjona, Bolívar, Col.	SEM

APPENDIX C. Locations of populations of *Aphelandra* species used in field and greenhouse studies: (O) = sites of field observations for flower visitors, (IC) = sources of greenhouse grown plants used in interpopulation crosses.

2. *A. sinclairiana*

Colón (O)—Panama, Colón: Pipeline Rd., 5 km from Gamboa, 50 m. (Now part of Parque Nacional Soberanía.)

3. *A. storkii*

Pto. Viejo (O)—Costa Rica, Heredia: Finca La Selva, ca. 6 km from Pto. Viejo, along Río Pto. Viejo, 100 m.

4. *A. gracilis*

El Valle (O)—Panama, Coclé: 10 km beyond El Valle de Antón, 800 m.

5. *A. golfodulcensis*

Corcovado (O, IC)—Costa Rica, Puntarenas: Corcovado National Park, Osa Peninsula, sea level.

San Vito (O, IC)—Costa Rica, Puntarenas: 6 km from San Vito de Java, forest below Las Cruces Botanical Garden, 1,200 m.

6. *A. panamensis*

Santa Rita (IC)—Panama, Colón: 25 km from Transisthmian Hwy., Santa Rita Ridge, 300 m.

Cerro Jefe (IC)—Panama, Panamá: 30 km above InterAmerican Hwy. on road to Cerro Jefe, 800 m.

Cerro Pirre (O, IC)—Panama, Darién: upper slopes of Cerro Pirre, about 12 km S of El Real, 600–800 m.

7. *A. deppeana*

Cañas (O, IC)—Costa Rica, Guanacaste: 8 km N of Cañas along InterAmerican Hwy., 50 m.

San Vito (IC)—Costa Rica, Puntarenas: 6 km from San Vito de Java, Las Cruces Botanical Garden, 1,200 m.

Palmar (IC)—Costa Rica, Puntarenas: 10 km SE (toward Panama) of Palmar N., along InterAmerican Hwy., 100 m.

8. *A. lingua-bovis*

Corcovado (O, IC)—Costa Rica, Puntarenas: Corcovado National Park, Osa Peninsula, sea level.

San Vito (O, IC)—Costa Rica, Puntarenas: 6 km from San Vito de Java, forest before Las Cruces Botanical Garden, 1,200 m.

Portobelo (IC)—Panama, Colón: near bridge over Río Buenaventura near town of Portobelo, sea level.

9. *A. leonardii*

Frailes (O, IC)—Costa Rica, San José, Río Tarrazú near Frailes, 1,300 m.

Cerro Pirre (IC)—Panama, Darién: lower slopes of Cerro Pirre, about 12 km S of El Real, 500 m.

11. *A. campanensis*

El Valle (O)—Panama, Coclé: 10 km beyond El Valle de Antón, 800 m.

El Copé (O)—Panama, Coclé: about 10 km past El Copé, 250 m.

12. *A. hartwegiana*

Río Pirre (O)—Panama, Darién: along Río Pirre about 12 km S of El Real, 400 m.

13. *A. darienensis*

Cerro Pirre (O)—Panama, Darién: upper slopes and summit of Cerro Pirre, about 12 km S of El Real, 800–1,300 m.

[illegible]

APPENDIX E. Character by taxon matrix. Species numbers and abbreviations as in Table 2, characters as in Table 13.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. TE	1	0	1	1	1	2	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0
2. SI	1	1	0	2	1	1	0	0	1	2	1	1	1	1	0	0	1	0	0	1	0
3. ST	0	1	0	2	1	1	1	0	1	3	0	1	1	1	0	0	1	2	0	1	1
4. GR	1	1	1	1	1	2	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0
5. GO	1	1	2	1	1	2	0	0	0	1	0	1	2	1	0	0	0	0	0	0	0
6. PA	1	2	1	2	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
7. DE	1	2	1	1	0	0	0	0	0	1	0	1	3	1	0	0	0	0	0	0	0
8. LB	0	0	1	0	0	2	2	0	1	2	0	0	0	1	0	0	1	2	0	1	1
9. LE	1	1	1	0	0	2	2	0	1	1	0	0	0	1	0	0	0	1	0	0	1
10. LA	0	0	1	0	0	2	2	1	1	1	0	0	0	0	0	0	1	1	0	1	1
11. CA	0	0	1	0	1	2	2	0	1	1	0	0	0	1	0	1	1	2	1	1	2
12. HA	0	0	1	0	1	2	2	0	1	2	1	0	0	2	0	2	1	3	1	1	2
13. DA	0	0	1	0	0	2	2	0	1	4	1	0	0	1	1	1	1	2	0	1	2
Ancestor	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0

APPENDIX E. Extended.

22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
1	2	0	2	2	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0
2	2	0	2	2	0	2	0	1	0	1	1	1	1	1	1	1	0	0	0	0	0
3	3	0	2	2	0	2	0	1	0	0	2	0	1	1	1	1	0	0	0	0	0
2	2	0	1	1	0	1	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0
2	2	0	1	1	0	2	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0
2	1	0	1	3	0	1	1	1	1	0	0	0	1	1	1	0	1	0	0	0	1
0	0	0	2	3	0	0	1	1	0	0	0	0	1	0	1	0	1	0	0	0	1
1	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0
2	2	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0
2	2	0	0	0	0	2	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0
2	2	0	0	0	0	2	0	0	0	0	1	0	0	2	0	1	0	1	1	1	0
2	3	0	0	0	1	3	0	0	0	0	2	0	0	2	0	1	0	1	1	1	0
2	3	1	0	0	0	3	0	0	0	0	3	0	0	2	0	1	0	1	1	1	0
1	2	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

APPENDIX F. Character state changes for phylogenetic hypothesis presented in Figure 58, by character and stem in which change occurs; characters and character states as in Table 13; and stem abbreviations as in Figure 58. Letters denote apparent type of evolutionary change: P = parallelism, R = reversal, A = derived character state unique to species, S = derived state shared by all distal taxa.

1. ST: 0 (R)	18. ST: 2 (P)
LE: 1 (P)	LB: 2 (P)
A: 1 (P)	HA: 3 (A)
2. TE: 0 (R)	G: 1 (P)
LB: 1 (P)	J: 2 (P)
DA: 1 (P)	19. DA: 0 (R)
F: 2 (S)	J: 1 (S)
H: 0 (R)	20. LE: 0 (R)
3. GO: 2 (A)	B: 1 (P)
C: 0 (S)	G: 1 (P)
4. PA: 2 (P)	21. ST: 1 (P)
A: 1 (S)	G: 1 (P)
C: 2 (P)	J: 2 (S)
5. DA: 0 (R)	22. TE: 1 (R)
A: 1 (P)	ST: 3 (A)
F: 0 (R)	DE: 0 (A)
J: 1 (P)	A: 2 (P)
6. AN: 2 (S)	H: 2 (P)
C: 1 (R)	23. ST: 3 (P)
F: 0 (R)	DE: 0 (A)
7. ST: 1 (P)	LB: 1 (P)
G: 2 (S)	F: 1 (P)
8. GR: 1 (P)	K: 3 (P)
LA: 1 (P)	24. DA: 1 (A)
9. AN: 1 (S)	25. DE: 2 (P)
D: 0 (R)	B: 2 (P)
10. ST: 3 (P)	G: 0 (S)
GR: 0 (A)	26. B: 2 (P)
LB: 2 (P)	F: 3 (S)
DA: 4 (A)	G: 0 (S)
C: 2 (P)	27. HA: 1 (A)
K: 2 (P)	28. GO: 2 (P)
11. ST: 0 (R)	DE: 0 (A)
B: 1 (P)	LB: 1 (P)
K: 1 (P)	C: 2 (P)
12. A: 1 (S)	G: 2 (P)
13. GO: 2 (P)	K: 3 (S)
DE: 3 (A)	29. F: 1 (S)
A: 1 (S)	30. A: 1 (S)
14. GR: 0 (P)	31. PA: 1 (P)
LA: 0 (P)	LB: 1 (P)
HA: 2 (A)	32. SI: 1 (A)
15. DA: 1 (A)	33. TE: 0 (R)
16. HA: 2 (A)	ST: 2 (P)
J: 1 (S)	DA: 3 (A)
17. LB: 1 (P)	A: 1 (P)
B: 1 (P)	F: 0 (R)
I: 1 (P)	J: 1 (P)
	K: 2 (P)

APPENDIX F. Continued.

34.	SI:	1	(A)
35.	A:	1	(S)
36.	DE:	0	(A)
	J:	2	(S)
37.	A:	1	(S)
38.	LB:	0	(R)
	AN:	1	(S)
	F:	0	(R)

39.	LB:	1	(P)
	F:	1	(P)
40.	H:	1	(S)
41.	H:	1	(S)
42.	I:	1	(S)
43.	F:	1	(S)
